

Ecomorphological analysis of aerial performance in a non-specialized lacertid lizard, *Holaspis guentheri*

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SUMMARY

Controlled aerial descent has evolved at least 30 times independently in different vertebrate and invertebrate lineages. A whole suite of morphological modifications, such as patagia, lateral skin folds and webbed feet, have been suggested to enhance descending ability. In this study, we compare aerial performance (i.e. vertical and horizontal velocity, horizontal distance covered, duration of descent) and morphology (body mass, body width, inter limb distance, surface area and wing loading) among three species of lizards, representing a range of aerial descenders present within the clade. Our performance measurements show that the lacertid *Holaspis guentheri* performs intermediately to the specialized gekkonid *Ptychozoon kuhli* and the rock-dwelling lizard *Podarcis muralis*. The small relative body mass of *H. guentheri* results in a low wing loading similar to that of *P. kuhli* thus enhancing its aerial performance. Whereas the latter generates great lift forces and is able to cover great horizontal distances, *H. guentheri*'s low wing loading seems to be responsible for a slow descent and low impact forces upon landing. Our results show that very small morphological changes may result in noticeable and ecologically relevant changes in performance.

Key words: biodynamics, ecomorphology, interspecific comparison, performance, wing loading.

INTRODUCTION

The invasion of novel and competitor-free habitats plays an important role in organismal diversification and adaptive variation (Grant, 1998; Schluter, 2000). An example of an extreme habitat transition is the one between terrestrial and aerial environments. The associated evolution of aerial locomotion is hypothesized to have progressed from jumping in an arboreal context to directed aerial descent, controlled gliding and ultimately powered flight (Maynard-Smith, 1952; Kingsolver and Koehl, 1994; Dudley et al., 2007). Being able to move through the air seems advantageous in several ways, particularly for arboreal animals. Firstly, arboreal animals must move through complex and dynamic environments high above the ground. Being able to slow down their descent, either by gliding or flying, will prevent them from getting injured when falling or jumping down (Emerson and Koehl, 1990; Schlesinger et al., 1993; Kingsolver and Koehl, 1994; Byrnes et al., 2008). Secondly, they are able to escape from arboreal or terrestrial predators (Emerson and Koehl, 1990; Kingsolver and Koehl, 1994; McCay, 2001; Yanoviak et al., 2005) and, at the same time, are able to pursue aerial prey (Emerson and Koehl, 1990; Kingsolver and Koehl, 1994). Lastly, the energetic cost of aerial locomotion has been predicted and shown to be lower than that of moving over ground, with aerial descent being energetically more efficient than powered flight (Norberg, 1983; Emerson and Koehl, 1990; Dial, 2003; McGuire and Dudley, 2005; Scheibe et al., 2006; Dudley et al., 2007; Byrnes et al., 2008).

Whereas active flight, powered by the flapping of wings, has evolved only in three extant lineages (i.e. birds, bats and insects), descending in a controlled fashion has evolved at least 30 times

independently in different vertebrate and invertebrate groups [e.g. mammals, reptiles, amphibians, insects (Dudley et al., 2007)]. The morphological modifications thought to enhance aerial performance range from the absence of any obvious aerodynamic surfaces in gliding snakes (see Socha, 2002) and ants (Yanoviak et al., 2005) to lateral folds in some gliding lizards and webbed feet in gliding frogs (Russell, 1979; Emerson and Koehl, 1990; Russell et al., 2001; McCay, 2001; Pough et al., 2004) to extensive patagia in flying squirrels (Jackson, 2000; Stafford et al., 2002) and *Draco* lizards (McGuire, 2003; McGuire and Dudley, 2005). Although several recent studies have quantified aerial performance, they have all focused on a single species or a set of closely related species with a similar morphology (e.g. McCay, 2001; Socha, 2002; Young et al., 2002; McGuire and Dudley, 2005; Yanoviak et al., 2005; Byrnes et al., 2008). To date, it remains largely unexplored how different morphologies associated with an aerial lifestyle translate into differential aerodynamic performance.

Historically, a distinction has been made between gliding and parachuting based on the descent angle relative to the horizontal (Oliver, 1951). Because the distinction is quite arbitrary and aerodynamic mechanisms of control are similar in both cases (Dudley et al., 2007), we will not make such a distinction here. Instead, we will follow Dudley et al.'s suggestion (Dudley et al., 2007) and use the term 'directed aerial descent' to mean any controlled descent by an organism that converts gravitational potential energy to useful aerodynamic work. In the present study we compare aerial performance among three lizard species; *Ptychozoon kuhli* Stejneger 1902 (Gekkota), *Holaspis guentheri* Grey 1863 (Lacertidae) and *Podarcis muralis* Laurenti 1768 (Lacertidae). We specifically selected

these three species as they represent a range of aerial descenders within the clade. Whereas *P. kuhli* is probably one of the most well known aerial lizards (Oliver, 1951; Russell, 1979; Russell et al., 2001; Young et al., 2002), anecdotal observations on *H. guentheri* suggest it is capable of moving from tree-to-tree using a controlled aerial descent (Schjötz and Volsøe, 1959; Dungen, 1967; Arnold, 1989; Arnold, 2002). The third species, *P. muralis*, is a typical climbing but non-aerial lizard (Arnold et al., 1978). In addition, the three species differ markedly with regard to the degree in which they possess morphological modifications for an aerial lifestyle. The well-studied *P. kuhli* possesses cutaneous head and body flaps and extensive webbing between the digits (Russell, 1979; Russell et al., 2001; Young et al., 2002; Pough et al., 2004). On the contrary, neither of the lacertids does. This is partially surprising as even the species presumed to be capable of making a directed aerial descent, *H. guentheri*, seems to lack obvious morphological modifications that enhance aerial ability. By comparing its aerial performance and related morphological and aerodynamical variables with those of an aerial lizard (*P. kuhli*) and a non-aerial close relative (*P. muralis*), we investigate whether, and how, small changes in morphology may potentially result in ecologically relevant functional changes. In a broader context, understanding the ecomorphological mechanisms used by *H. guentheri*, lacking gross morphological modifications, to slow down, control and orient its descent may shed light on the transitional stages in the evolutionary pathway towards vertebrate flight.

We specifically address the following questions: (1) how well does *H. guentheri* perform while descending and (2) which morphological characteristics may explain *H. guentheri*'s aerial performance? To answer the former question, we quantify four measures of aerial performance (i.e. horizontal distance covered, duration of descent, horizontal and vertical velocity upon landing) and compare it with the aerial performance of a true glider, *P. kuhli*, and the non-aerial *P. muralis*. By comparing the morphology of the three species (i.e. mass, body width, inter limb distance, surface area, wing loading) and two aerodynamical factors while descending (i.e. lift and drag coefficient), we address the latter question.

MATERIALS AND METHODS

Animals

Specimens of *H. guentheri* and *P. kuhli* individuals were obtained from the pet trade whereas the *P. muralis* individuals were captured by hand or noose near Hotton (Belgium). We housed the animals in glass terraria (width \times length \times height = 0.50 \times 0.50 \times 1.00 m) with species kept apart. A single terrarium held no more than 10 individuals of *H. guentheri* and *P. muralis* and no more than three individuals of *P. kuhli*. A 100 W light bulb above each terrarium provided heat and light for 8 h per day. Sand, leaf litter, twigs, plants and rocks were placed in the terraria to provide basking spots and shelter. We fed the animals calcium-dusted crickets (*Acheta domestica*) once a week and water was provided *ad libitum*.

Morphometrics

We measured the following variables with digital calipers [Mitutoyo CD-15DC, Mitutoyo (UK) Ltd, Telford, UK] to the nearest 0.01 mm for all animals used in the performance trials (see below): snout-vent length (SVL), inter limb distance and body width, measured at mid-body. The latter variable was measured three times and the median value was used in subsequent analyses. The lizards were weighed to the nearest 0.01 g on an electronic balance (FX-3200, A&D Company, Tokyo, Japan).

We quantified the surface area of a descending lizard in the following way. All lizards were filmed dorsally with a high-speed

camera (250 Hz; Redlake MotionPro 500, Tallahassee, FL, USA) positioned above a take-off platform at a height of 2.5 m while descending. The camera was positioned such that the lizards were in view from take-off to landing. Out of each video sequence, we selected the frame in which the body of the lizard was maximally laterally extended. Using tpsDig (F. J. Rohlf, SUNY, Stonybrook, NY, USA), we outlined the outer edges of the body between the limb pairs and calculated the surface area. Because *P. kuhli* possesses webbed feet, we quantified the surface area of the four feet in a similar way and summed all surface areas (i.e. four feet and body). We used the known inter limb distance of each respective individual lizard as the scaling factor. As a measure of maximal surface area for each individual, we used the highest value for that individual out of the different jump trials. We subsequently divided body mass by surface area to estimate wing loading for each individual. We were able to get reliable estimates of surface area while descending of four *H. guentheri* individuals, six *P. kuhli* and six *P. muralis* individuals.

X-rays synchrotron propagation phase contrast microtomography

We used the BM05, ID17 and ID19 beamlines of the European Synchrotron Radiation Facility (ESRF) to obtain data of the three studied species (Betz et al., 2007; Du Pasquier et al., 2007). We acquired tomographic data from two specimens of *H. guentheri* (energy of 25/52 Kev, with a propagation distance of 700/5000 mm and a voxel size of 5.04/30 μ m), one *P. kuhli* (30 Kev, 862 mm, 40.48 μ m) and one *P. muralis* (40 Kev, 900 mm, 14.93 μ m). Three-dimensional renderings were obtained after semi-automatic segmentation of the skeleton, using Avizo 6.0 (Mercury Computer Systems, Chelmsford, MA, USA) and VGStudio MAX 2.0 (Volume Graphics GmbH, Heidelberg, Germany).

Performance variables

In a first set of experiments, we quantified the aerial performance of the different lizards. Animals were filmed in lateral view at 50 Hz (Panasonic AG 455 video camera, Panasonic Europe Ltd, Berks, UK) while jumping from a platform attached 2 m above the ground. The camera was positioned at a distance of 3.5 m from the platform to ensure that both the platform and landing area were in view. The landing area consisted of a 2.45 \times 2.43 m enclosed arena. Side walls, 0.60 m high, prevented the animals from escaping, and soft padding on the floor prevented injury upon landing. If lizards did not jump voluntarily, we induced them to jump off the platform by tapping the platform and/or the base of the lizard's tail. We conducted performance trials over the course of several days, with no more than three trials per day per individual. In total, six *H. guentheri* individuals jumped 12 times each ($N_{\text{total}}=72$ jumps), five *P. kuhli* individuals eight times each ($N_{\text{total}}=40$) and 10 *P. muralis* individuals 11 times each ($N_{\text{total}}=110$).

We subsequently screened all movies and omitted sequences that did not meet the following criteria: (1) path of lizard planar and perpendicular to the camera, (2) lizard actually jumped (as opposed to falling from the platform) and (3) was in view during the whole jump/descent. After selection, we retained 15 jumps from four *H. guentheri* individuals, 13 jumps from five *P. kuhli* individuals and 42 jumps from nine *P. muralis* individuals. In these sequences, we digitized the tip of the snout of the lizard frame-by-frame, using a NAC XY coordinator and custom-written software in Qbasic (custom-written by P.A.). Digitization started from the moment the lizard took off from the platform and ended at the moment it landed on the padding. To be able to transform

the XY -coordinates in pixels into coordinates in meters, we digitized a reference grid of known dimensions, recorded when positioned in the descending plane.

After digitization, we filtered all data using a zero phase shift low-pass fourth order Butterworth filter, using a cut-off frequency of 7 Hz (Borland C 3.1.; custom-written by P.A.). The same program was used to calculate horizontal and vertical velocity by numerical differentiation. As the filtering procedure may have caused artificial deflections of the filtered signal at the beginning and end of each digitized sequence, we used displacement and velocity data at a height of 1.9 m and 0.1 m as 'starting' and 'landing' values, respectively, in further analyses.

Based on the filtered data, we calculated four performance variables: (1) horizontal velocity at 'landing' (v_{hor}), (2) vertical velocity at 'landing' (v_{ver}), (3) horizontal distance covered, i.e. the difference in displacement along the X -axis between the start and end of a jump/descent and (4) duration of the descent. To test whether the animals were actually descending in a controlled fashion instead of just falling, we compared the values of the four performance variables with theoretical values obtained by modeling each sequence as if the lizard were moving in a vacuum (hereafter referred to as 'model'). For each sequence, we used the position and velocities at a height of 1.9 m of the lizard as input variables. With only gravity acting (horizontal forces are absent in the vacuum), the horizontal velocity of the model is constant over the course of the fall. XY -coordinates of the lizard (treated as a point mass in this case) and its vertical velocity were subsequently recalculated by simple Eulerian numerical integration at 0.02 s time intervals. As an estimate of an animal's performance we used the difference between the values obtained for the real lizard and the values obtained for the model for horizontal velocity at 'landing', vertical velocity at 'landing', horizontal distance covered and duration of the descent. We used the differences in performance between the real lizard and the model as input for the statistical analyses (see below).

Aerodynamic variables

In a second set of experiments, we quantified two aerodynamic variables (i.e. lift and drag forces). Lift and drag forces acting on a gliding lizard (perpendicular to and aligned with its path of descent, respectively) reduce the sinking speed. At steep angles of descent, the drag force is most important. The more the lift force is involved in this retarding effect, the shallower the glide angle will be.

Determining lift and drag coefficients for each of the species provide an estimate of the capacity to counter the effect of gravity, independent of actual size and actual gliding speed. These coefficients could thus be regarded as an estimate of the aerodynamic adaptation. As lateral view high-speed recordings revealed a constant velocity for the final part of the descent in all three species (see further for details), they allow for a reliable estimation of the lift and drag coefficients. Based on the equations of motion, a constant velocity implies that the sum of all vertical and horizontal forces acting on the animal's body center of mass (bodyCOM) must equal zero. In case of a directed aerial descent, this can only be achieved when:

$$\mathbf{L} + \mathbf{D} + \mathbf{W} = 0, \quad (1)$$

where \mathbf{L} =lift force, \mathbf{D} =drag force and \mathbf{W} =body weight.

As a result, the magnitude of the lift and drag vector must equal:

$$\mathbf{L} = -mg\cos(\alpha) \quad (2)$$

$$\mathbf{D} = -mg\sin(\alpha), \quad (3)$$

where m =body mass, $g=-9.81 \text{ ms}^{-2}$ and α =angle of descent path relative to horizontal). Hence, lift (C_L) and drag (C_D) coefficients are given by:

$$C_L = -mg\cos(\alpha) / (1/2\rho AV^2), \quad (4)$$

$$C_D = -mg\sin(\alpha) / (1/2\rho AV^2), \quad (5)$$

where ρ =density of air= 1.2 kg m^{-3} , A =surface area and V =descent speed.

The experimental set-up was similar to the one used to quantify aerial performance, except that filming was done with a high-speed video camera (PCI 1000S Redlake Imaging Motionscope) at 250 Hz recording only the last 0.60 m of the descent prior to landing thus allowing us to zoom in on the descending specimens. In this experiment, seven *H. guentheri*, eight *P. kuhli* and nine *P. muralis* individuals were used, performing five jumps each.

Using Didge Image Digitizing Software (A. J. Cullum), we digitized four points (tip of the snout, pectoral girdle, pelvic girdle and tail tip) on the animal, frame-by-frame, for all sequences meeting the criteria outlined above. Sequences for which we were unable to digitize all four points over the last 0.60 m of the descent prior to landing were removed from further analyses. Because of our stringent selection criteria, only six jumps performed by two *H. guentheri*, eight jumps by two *P. kuhli* and 17 jumps by six *P. muralis* individuals were retained for further analyses.

Because the calculation of the lift and drag coefficients is based on the displacement of the total centre of mass (bodyCOM), we first needed to estimate the position of the bodyCOM in each frame of each sequence. We did so in the following way.

Based on the XY -coordinates of the tip of the snout, pectoral girdle, pelvic girdle and tail tip, we recalculated for each video frame the position of the COM of each segment separately. We assumed that the COM of the head, with its flattened conical shape tapering towards the snout tip, is positioned on the axis 'snout-pectoral girdle' 2/3 of the distance from the tip of the snout to the pectoral girdle; the COM of the body is assumed to be positioned halfway along the axis 'pectoral-pelvic girdle'; the COM of the tail, regarded as an elongated distally tapering cone, is assumed to be at 1/3 of the distance from the pelvic girdle to the tip of the tail.

The head and tail of one dead specimen of each species were separated from the body with the limbs (i.e. three segments). We subsequently weighed each of the segments on an electronic balance (FX-3200, A&D Company) to the nearest 0.01 g and expressed these as a fraction of total body mass. Segmental masses of the filmed individuals could thus be estimated on the basis of their total mass and the fractions.

For each frame, we subsequently estimated the position of the bodyCOM of the whole animal in both the X and Y direction using the following formulae:

$$X_{\text{bCOM}} = [(X_{\text{hCOM}} \times \text{mass}_h) + (X_{\text{trCOM}} \times \text{mass}_t) + (X_{\text{taCOM}} \times \text{mass}_{\text{ta}})] / \text{total mass}_b \quad (6)$$

and

$$Y_{\text{bCOM}} = [(Y_{\text{hCOM}} \times \text{mass}_h) + (Y_{\text{trCOM}} \times \text{mass}_t) + (Y_{\text{taCOM}} \times \text{mass}_{\text{ta}})] / \text{total mass}_b, \quad (7)$$

where X_{bCOM} and Y_{bCOM} =position of the bodyCOM; X_{hCOM} and Y_{hCOM} =position of the headCOM; X_{trCOM} and Y_{trCOM} =position of the trunkCOM; X_{taCOM} and Y_{taCOM} =position of the tailCOM; mass_h =mass of head; mass_t =mass of trunk; mass_{ta} =mass of tail; total mass_b =total mass of body.

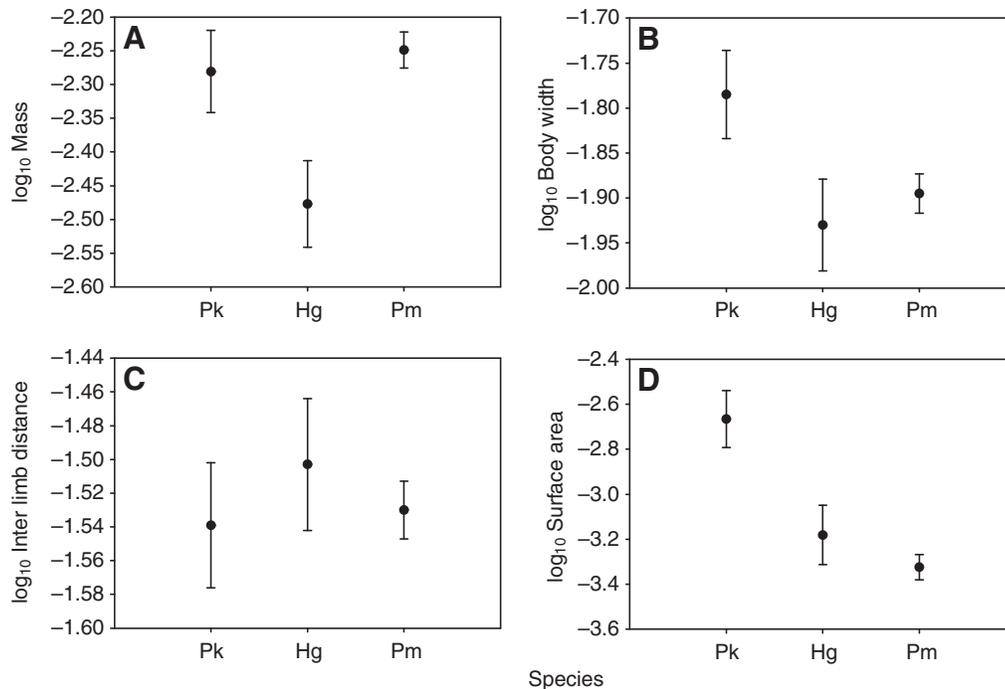


Fig. 1. Estimated marginal means [snout–vent length (SVL) entered as co-variate] per species of (A) body mass, (B) body width, (C) inter limb distance and (D) surface area. Relative body mass and surface area differ significantly among species. Error bars represent one standard error. Pk=*Ptychozoon kuhli*, Hg=*Holaspis guentheri*, Pm=*Podarcis muralis*.

We used the regression coefficient of the linear regression of X_{bCOM} and Y_{bCOM} against time as an estimate of horizontal and vertical velocity over the last 0.60 m of the descent, respectively. All regression coefficients were above 0.97, proving speeds were nearly constant. Total velocity was calculated as the result of horizontal and vertical velocity. The angle of the descent path (α) was estimated as the arctangent of the regression coefficient of the linear regression of the position of Y_{bCOM} against X_{bCOM} .

Statistical analyses

Prior to statistical analyses, all morphological, performance and aerodynamic variables were logarithmically (\log_{10}) transformed. We used SPSS 15.0 (SPSS Inc., Chicago, IL, USA) to perform all statistical analyses.

To test whether the three species differ morphologically, we performed a multivariate analysis of covariance (MANCOVA) in which we entered species as the factor; mass, body width, inter limb distance and surface area as dependent variables; and SVL as the covariate. As slopes, represented by the $SVL \times$ species interaction term, did not differ among species ($P=0.85$), we removed the interaction effect from the final model. A one-way analysis of variance (ANOVA), with species entered as the factor, was used to test whether wing loading differed among the three species.

To test whether the three species differ in relative aerial performance (i.e. the differences in horizontal and vertical velocity, horizontal distance and duration of descent between the real lizard and the model) and the aerodynamic variables associated with descending (i.e. lift and drag coefficient), we performed nested ANOVAs for each variable separately. In these nested ANOVAs, species and individual nested within species were used as factors.

RESULTS

Morphometrics

In the MANCOVA for which species was entered as factor, SVL as covariate and mass, body width, inter limb distance and surface area as dependent variables, both species ($F_{8,20}=4.34$, $P=0.004$) and SVL ($F_{4,9}=9.99$, $P=0.002$) had a significant effect. Subsequent one-

way analyses of covariance (ANCOVAs) revealed that species differ significantly with respect to mass and surface area (both $P<0.0001$) (Fig. 1A,D) but not in body width or inter limb distance (both $P>0.27$; Fig. 1B,C). *Holaspis guentheri* has the smallest relative mass and *P. muralis* the highest (Fig. 1A). Surface area is greatest for *P. kuhli* and smallest in *P. muralis* (Fig. 1D). The covariate had a significant effect on mass and inter limb distance (both $P<0.002$) but not on body width or surface area (both $P>0.15$).

The one-way ANOVA with wing loading as the dependent variable and species as the factor revealed a significant difference among species ($F_{2,13}=31.67$, $P<0.0001$). Whereas *P. kuhli* and *H. guentheri* have a similar, very low, wing loading, *P. muralis* has a much higher wing loading (Fig. 2).

Performance

In all four nested ANOVAs with species and individual nested within species as factors and the performance variable as the dependent

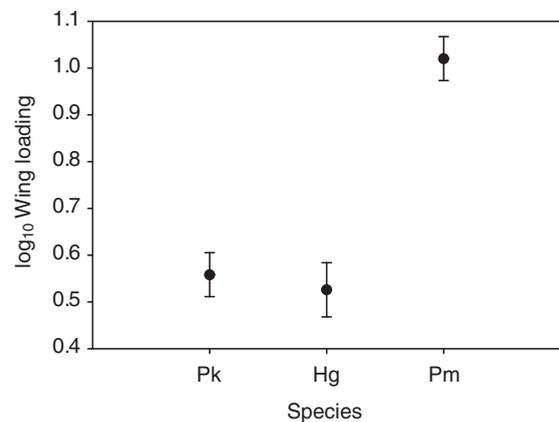


Fig. 2. Mean wing loading (i.e. ratio of body mass to surface area) per species. Wing loading differs significantly among *Ptychozoon kuhli* (Pk), *Holaspis guentheri* (Hg) and *Podarcis muralis* (Pm). Error bars represent one standard error.

Table 1. Output of nested ANOVAs testing for differences in performance of a gliding animal and a falling, frictionless ball (i.e. difference in horizontal velocity upon landing, v_{hor} ; difference in vertical velocity upon landing, v_{ver} ; difference in horizontal distance covered; difference in duration of glide)

Dependent	Effect	d.f.	F	P
$\log_{10} v_{hor}$	Intercept	1, 51	0.001	0.97
	Ind(species)	15, 51	1.18	0.32
	Species	2, 51	4.11	0.02
$\log_{10} v_{ver}$	Intercept	1, 51	140.49	<0.0001
	Ind(species)	15, 51	0.78	0.69
	Species	2, 51	7.19	0.002
\log_{10} Horizontal distance	Intercept	1, 51	6.07	0.02
	Ind(species)	15, 51	0.83	0.65
	Species	2, 51	6.43	0.003
\log_{10} Duration of descent	Intercept	1, 51	3823.44	<0.0001
	Ind(species)	15, 51	0.98	0.49
	Species	2, 51	18.00	<0.0001

Both individual nested within species, i.e. ind(species) and species were entered as main effects. Significant main effects are shown in bold.

variable, the effect of individual nested within species was non-significant (all $P > 0.32$; Table 1). However, the difference with the model for horizontal velocity, vertical velocity, horizontal distance covered and duration of the descent all differed significantly among species (all $P < 0.02$; Table 1). The difference in horizontal velocity between the lizard and the model was smallest, but positive, in *P. kuhli*, and greatest in *P. muralis*, suggesting that *P. muralis* is the least capable of decreasing its horizontal velocity during its descent

(Fig. 3A). The difference in vertical velocity was greatest, and negative, between *P. kuhli* and the model, followed by *H. guentheri*. The difference in vertical velocity between *P. muralis* and the model was smallest (Fig. 3B). In addition, the difference in distance covered and duration of the descent was greatest, and positive, between the model and *P. kuhli*, and smallest in *P. muralis*. Values for *H. guentheri* were intermediate (Fig. 3C,D).

Aerodynamic variables

The two nested ANOVAs with the aerodynamic variables (i.e. lift and drag coefficient) as dependent variables and species and individual nested within species entered as factors, showed that the effect of individual nested within species was significant in both cases (lift coefficient: $F_{7,21}=3.68$, $P=0.010$; drag coefficient: $F_{7,21}=7.91$, $P<0.0001$); thus, suggesting individual variation is substantial. At the species level, *P. kuhli*, *H. guentheri* and *P. muralis* also differed significantly with respect to both the lift coefficient ($F_{2,21}=19.90$, $P<0.0001$) and the drag coefficient ($F_{2,21}=41.96$, $P<0.0001$). The lift coefficient is greatest for *P. kuhli*, intermediate for *P. muralis* and smallest for *H. guentheri* (Fig. 4A). The drag coefficient, on the contrary, is the greatest for *P. muralis* and similar in *H. guentheri* and *P. kuhli* (Fig. 4B).

DISCUSSION

Our results show that *H. guentheri* is capable of making a controlled aerial descent as it performs better than the model lizard (i.e. moving in a vacuum). When compared with the other two lizards, its aerial ability (i.e. horizontal and vertical velocity, horizontal distance covered, duration of descent) is intermediate. It clearly has a greater aerial performance than its relative *P. muralis* but is inferior to the true glider, the gekkonid *P. kuhli*.

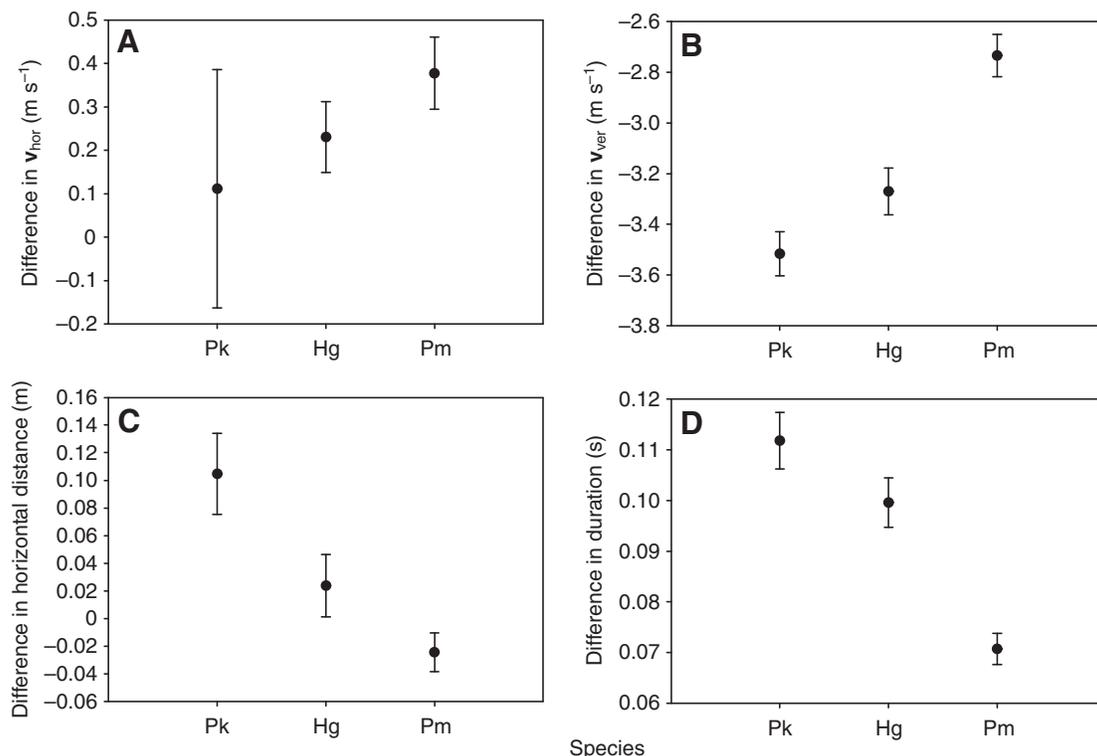


Fig. 3. Mean difference in performance between the lizard and the model: (A) horizontal velocity upon landing (v_{hor}), (B) vertical velocity upon landing (v_{ver}), (C) horizontal distance covered and (D) duration of the descent. All four performance measurements differ significantly among species. Error bars represent one standard error. Pk=*Ptychozoon kuhli*, Hg=*Holaspis guentheri*, Pm=*Podarcis muralis*.

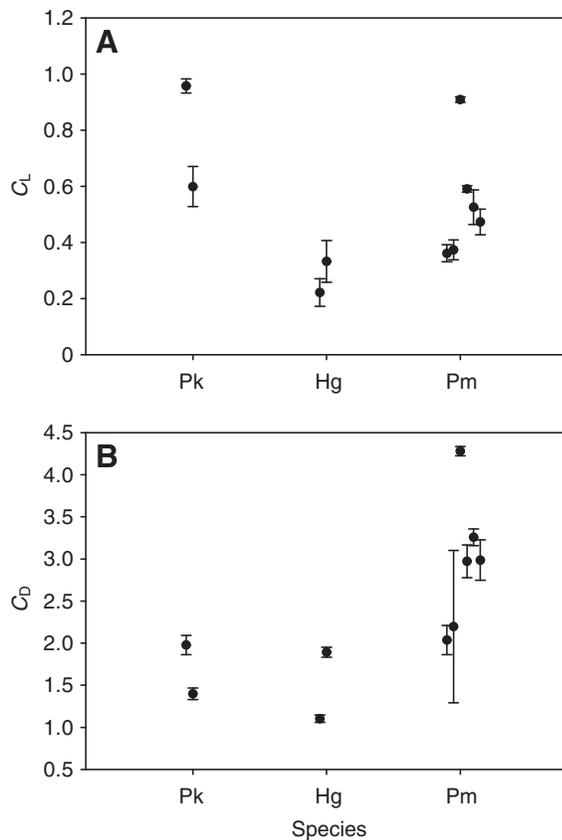


Fig. 4. Mean per individual of (A) lift coefficient (C_L) and (B) drag coefficient (C_D). Individuals are grouped per species and shown offset for clarity reasons. Both aerodynamic variables vary significantly among individuals within species and among species. Error bars represent one standard error. Pk=*Ptychozoon kuhli*, Hg=*Holaspis guentheri*, Pm=*Podarcis muralis*.

Whereas aerial frogs can be distinguished from non-aerial frogs by a unique set of morphological features and the absence of intermediate forms (Emerson and Koehl, 1990), our results concerning the morphological differences among the three lizard species under study here are quite different. For example, we found that *H. guentheri*, *P. kuhli* and *P. muralis* do not differ significantly with respect to relative body width or inter limb distance. However, relative body mass and surface area do differ significantly, although the latter is similar in both lacertids. This is surprising as it has been suggested previously that, compared with other lacertids, *H. guentheri* is capable of expanding its body laterally to a greater degree by rotating its exceptionally long dorsal ribs forward (Dunger, 1967; Arnold, 1989). Our measurements of maximal surface area, which were taken during descending, do not corroborate the idea that the elongated ribs of *H. guentheri* result in a greater functional aerodynamic surface area. Instead, the most striking morphological modification of *H. guentheri* appears to be a small body mass. Similarly, *Anolis carolinensis* has been suggested to be slightly better at descending in a controlled fashion (measured as the deviation from the vertical line) compared with another arboreal lizard species, *Sceloporus undulatus*, because of its lower body mass (Oliver, 1951). Some skeletal and osteological characteristics typical of *H. guentheri* may explain how it achieves such a low body mass. For instance, compared with other lacertids, the skull and girdles appear to be less massive, thinner and delicate, with more extensive foramina in *H. guentheri* (Arnold, 1989; Arnold, 2002) (see Fig. 5).

These small scale morphological modifications may play a role in reducing overall body mass. In contrast to both lacertids, *P. kuhli* is characterized by a much more heavily ossified skeleton; thus, contributing to its greater body mass, which is offset however by its increased surface area (Figs 1 and 5).

In addition, when comparing the lift and drag coefficients for the three species, we found that the former is greatest in the gekkonid, *P. kuhli* whereas the latter is greatest in the non-aerial lizard, *P. muralis*. Because the individual variation within species is substantial, we realize that the aerodynamic differences among species should be interpreted with caution. However, our results suggest that *P. kuhli* is able to generate lift, slow down its descent and cover greater distances. *Holaspis guentheri*, on the contrary, does not seem to be capable of generating lift or drag, although the performance measurements show it is capable of slowing down its descent. The fact that *P. muralis* has the greatest drag coefficient does not translate into an increase in its aerial performance. This seems contradictory but as the surface area in both lacertids is similar, the differences in aerial performance can only be explained by the difference in body mass. The relatively light mass of *H. guentheri* will result in it reaching an equilibrium between the upward and gravitational forces earlier in the descent, i.e. at a lower falling speed, than *P. muralis*. This finding corroborates the idea that *H. guentheri* is capable of descending in a controlled fashion, not because of intrinsic aerodynamic adaptations but solely because of its relatively small body mass.

By combining a low mass and a *P. muralis*-like surface area, *H. guentheri* achieves a low wing loading, surprisingly similar to that observed for *P. kuhli*. Both species achieve a similar wing loading in a different way, however. Whereas for *H. guentheri* wing loading is low because of a great reduction in body mass, it is low in *P. kuhli* because of the large surface area created by the lateral skin flaps and webbed feet. Although the exact function and contribution of the flaps and webbed feet to the aerial performance and lift production in *P. kuhli* remains open to debate (cf. Marcellini and Keefer, 1976; Young et al., 2002), they may aid in generating high lift forces as the large effective aerofoil improves the lift to drag performance of the body as a whole (Rayner, 1981; Vogel, 2003; Pough et al., 2004; Dudley et al., 2007). The low body mass for a given surface area of *H. guentheri* seems to slow down its descent, makes it stay aloft for a longer time and lowers the impact forces upon landing (Emerson and Koehl, 1990; Vogel, 2003; Pough et al., 2004). Our performance measurements corroborate this idea as vertical velocity and the duration of descent seem to be the performance variables most profoundly affected. For *P. kuhli*, apart from the decrease in vertical velocity and increase in duration of descent, horizontal distance covered is greater due to the larger lift forces (Vogel, 2003; Pough et al., 2004). As landing forces seem to decrease with descended distance, covering greater distances reduce the risk of injury upon landing (Byrnes et al., 2008). Thus, despite its large body mass, *P. kuhli* can land at least as softly as *H. guentheri*, as it combines a relatively large surface area with a great lift coefficient.

From an ecological perspective, the three species under study differ with respect to their distribution and microhabitat use. As for most aerial vertebrates, *P. kuhli* inhabits the Asian tropical forest (Pough et al., 2004) whereas *H. guentheri* occurs in African tropical forest (Schj tzt and Vols e, 1959; Dunger, 1967; Arnold, 1989; Arnold, 2002). *Podarcis muralis* is a typical European lacertid, occurring mainly in the vegetation, on small rocks and stone walls (Arnold et al., 1978). Because being capable of descending in a controlled fashion is more beneficial and ecologically relevant in

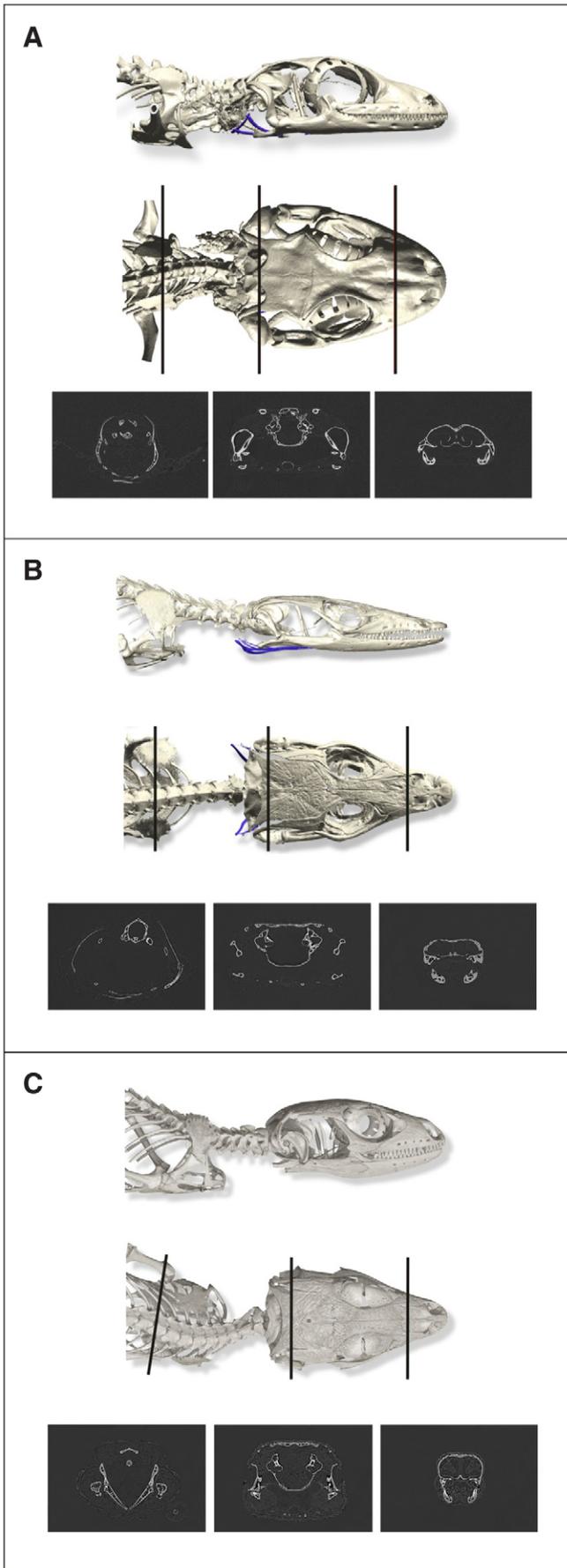


Fig. 5. Figure illustrating differences in morphology for the three different species: (A) *Ptychozoon kuhli*, (B) *Holaspis guentheri* and (C) *Podarcis muralis*. Illustrated are a lateral and a dorsal view for each species. Vertical lines illustrate the level of the virtual sections indicated below the volume renderings. Note the lower degree of ossification and slender build of *H. guentheri* compared with the other species.

arboreal animals, often moving around high above the ground (Emerson and Koehl, 1990; Dudley et al., 2007), it is not surprising that *P. muralis* is the worst aerial performer of the three species. Moreover, the differences in aerial performance between *H. guentheri* and *P. kuhli* may be interpreted in light of the structural differences between Asian and African tropical forests. In general, Asian tropical forests consist of higher trees but have a low liana density at crown height, compared with other tropical forests (Emmons and Gentry, 1983; Dudley and DeVries, 1990; LaFrankie et al., 2006; Corlett, 2007). Because *P. kuhli* occurs in Asian tropical forests, being able to make directed aerial descents and cover large distances may be selected for as it would allow *P. kuhli* to move from tree-to-tree with one leap, resulting in substantial energetic advantages (Dudley and DeVries, 1990). In African tropical forest, on the contrary, liana density is very high, often interconnecting tree crowns; thus, providing a pathway for arboreal animals (Emmons and Gentry, 1983; Dudley and DeVries, 1990). Although being able to slow down the descent, resulting in a softer landing, may still be advantageous (i.e. to avoid injuries), covering large distances may not be selected for in this specific ecological setting. Our results on *H. guentheri*'s aerial performance corroborate this idea.

Conclusion

Our results show that *H. guentheri*'s aerial ability is intermediate to that of the aerial gekkonid *P. kuhli* and a rock-dwelling lacertid *P. muralis*. A small body mass and a relatively low wing loading are responsible for *H. guentheri*'s relatively good aerial performance by slowing down its descent and reducing impact forces upon landing. Although morphological changes are small, they result in a noticeable change in an ecologically relevant function. As has been previously shown in other taxa [e.g. ants (Yanoviak et al., 2005); snakes (Socha, 2002)], our results corroborate the idea that arboreal animals do not necessarily need obvious morphological or aerodynamic modifications to be capable of (some form of) descending in a controlled fashion (Oliver, 1951; Dudley et al., 2007). Additionally, behavioral adjustments (e.g. body orientation) while falling may already suffice to slow down the rate of descent (Dudley et al., 2007). Although behavioral data are currently lacking for the three species under study here, it is not unthinkable that behavioral changes, followed by small scale morphological changes, may represent the first evolutionary steps towards an aerial lifestyle.

LIST OF ABBREVIATIONS

<i>A</i>	surface area
ANCOVA	analysis of covariance
ANOVA	analysis of variance
bodyCOM	body center of mass
C_D	drag coefficient
C_L	lift coefficient
D	drag force
<i>g</i>	gravitational acceleration
L	lift force

m	body mass
MANCOVA	multivariate analysis of covariance
mass _h	mass of head
mass _{ta}	mass of tail
mass _{tr}	mass of trunk
SVL	snout-vent length
total mass _b	total mass of body
V	descent speed
v_{hor}	horizontal velocity at landing
v_{ver}	vertical velocity at landing
W	body weight
X_{bCOM}, Y_{bCOM}	position of body COM
X_{hCOM}, Y_{hCOM}	position of the head COM
X_{taCOM}, Y_{taCOM}	position of the tail COM
X_{trCOM}, Y_{trCOM}	position of the trunk COM
α	angle of descent
ρ	density of air

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