Escape tendency and the mobility behavior of four alpine rodents do not change with altitude

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Abstract Behavioural responses are particularly important to quantify species-specific habitat influences on natural selection. Mountains, with their wide range of habitats, can be regarded as a valuable context where the environmental conditions influence animal behaviour. We studied the inter-specific variation in the escape tendency and the mobility behaviour in four alpine rodents' species, a bank vole (*Clethrionomys glareolus*) and three *Apodemus* mice, to evaluate the level of boldness and its variation with elevation. Analyses with generalized linear models revealed that the two groups of rodents (*Clethrionomys* vs. *Apodemus*) differed in both these traits. During arena tests, the latency time to first jump, an index of escape behaviour, was approximately 42% lower in *Apodemus* than in *C. glareolus*, in which 46.2% of individuals did not jump during the whole experiment. Also, the mobility, measured as the distance travelled, was 55% lower in *C. glareolus* compared to *Apodemus*. However, the leave-one-out cross validation did not detect any effect of elevation, neither on the distance travelled, nor on the latency time to the first jump. The apparent absence of elevation influence on the behaviors here considered, could indicate the presence of a genetic basis that regulates their expression in such species. These results can be interpreted in the context of differential habitat use and microhabitat segregation due to interspecific competition. In fact, the differentiation of niches (spatial, trophic and temporal) between the two taxa may have led to differences in behavioural traits.

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Introduction

Mammals exhibit behavioural responses to limiting factors, such as anthropogenic activities [1], or food resources [2], which may be important for understanding species adaptation, particularly in the context of environmental changes [3][4][5]. The first response by animals to a changing environment is predominantly through modification of their behaviour [6]. Foraging behaviour, predator avoidance, dispersal, migration, and reproduction are all factors directly affected by the environment [7], which in turn influences population dynamics, species interactions and community structure [4][8].

Mountains, characterized by pronounced habitat variability over small geographic distances, represent a valuable context in which environmental conditions may influence animal behaviour. As altitude increases primary productivity usually decreases, as well as temperature, duration of vegetative period and biomass, and plant phenology is delayed [9]. Consequently, at high elevations energetic resources are reduced and spatially and temporally scattered, and the structure and diversity of vegetation decrease [10][11][12]. Such habitat conditions can enforce behavioural responses on animals [13], by imposing levels of foraging and exposure to predators during animals' daily activities [14].

The so-called "bold-shy" continuum, which represent the degree of risk-prone behaviour [15][16][17], has been found to have an adaptive value in face of rapidly changing environmental conditions (e.g., rodents)[18]. Bold behaviors are associated with animals having a high level of general mobility, being more exploratory and risk-taking [19], and exhibiting greater aggression [20]. In contrast, shy behaviors are associated with animals with a high level of neophobia (avoidance of new object and experiences), with comparatively lower levels of activity and general mobility, and with low risk-taking [21][22][23].

Rodents, with their early reproductive age [24], high reproductive rates [25] and usually fast life histories [26], are suitable models for studying environmental effects on behaviors. These characteristics make rodents particularly responsive to selective pressures on fitness-related behavioural traits [18], at fine spatial [27] or across short temporal scales [28].

To evaluate whether the altitudinal distribution of the species determines their behavioural characteristics, here we analyzed two behaviors, escape tendency and mobility, in four sympatric rodents co-occurring in the Western Italian Alps across the elevation gradient (400 to 1,800 m a.s.l.): the bank vole *Clethrionomys glareolus* [29] and three *Apodemus* mice (the yellow-necked mouse *A. flavicollis* Melchior, 1834 , the wood mouse *A. sylvaticus* Linnaeus, 1758, and the alpine field mouse *A. alpicola* Heinrich, 1952; Fig.1). We predicted that elevation would have a non-neutral effect on the frequency of boldness-related traits in different species. In fact, we expected (H_1) that at high altitudes, where food resources can often become rarer and patchier, we would observe an increase in mobility which could be advantaged in such conditions [12]. We also predicted that (H_2) species distributed in different habitat type, such as *C. glareolus*, which are adapted to diverse and variable environmental conditions [30][31][32], would have shown high inter-specific variability in the level of boldness. In fact, these adaptations would allow them to respond more quickly to variable and changing environments [33]. Finally, we predicted a sex-dependent effect on boldness, as previously found for *A. flavicollis* [34], where males are more exploratory than females given their greater reproductive potential (H_3).

Materials and methods

Study area and animal manipulation

The study area was located in the Piedmont region (North-western Italy), within the territory of the Gran Paradiso National Park and its surroundings. Twelve trapping sites were identified and distributed along an elevation gradient, from 400 to 1822 m a.s.l (Table A1). At each trapping site, a line of 30 live traps (Sherman traps, 229 x 89 x 76 mm in size), located every 10 m, was placed, and the elevation was registered (using a GPS Garmin Etrex 32x). Traps were set up in the field for one week and checked at dawn and dusk, being baited with apple, sunflower seeds, and peanut butter, and provided with cotton as bedding

Animals were captured between the 15th of April and the 15th of September 2020, during the breeding season of the target species. Trapping days were randomly alternated at high and low altitude sites to avoid the effect of delay in seasonality along the altitudinal gradient. Trapped animals were marked with fur-clipping, sexed and weighted. Adult individuals (excluding evidently pregnant or lactating females) of the trapped species (e.g., based on fur characteristics and body dimensions [35]) with a minimum body weight of 15 g for *Apodemus* spp. and 13 g for *C. glareolus*, were selected for the behavioural experiments to reduce potential effects of body growth and ontogeny on the expression of behavioural traits [36][37]. Captured animals were transported to the closest of the three available laboratories (located at 497 m, 972 m, and 1065 m a.s.l.; Table A1). Tissue ear samples were collected and used in genetic bar coding of the three *Apodemus* species discrimination.

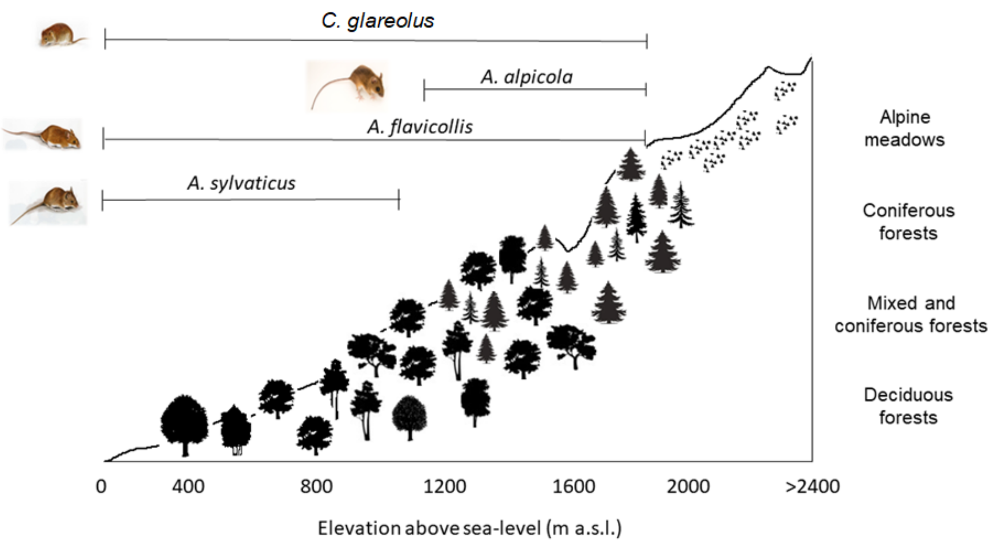

Figure 1: Distribution of deciduous, mixed and coniferous forests and study species (*Apodemus flavicollis*, *A. sylvaticus*, *A. alpicola* and *Clethrionomys glareolus*) across elevational gradient (400 to 1,822 m. a.s.l.) in Alps. Bars represent the altitudinal distribution where species were captured.

Animals were kept in captivity in individual cages with food and water at libitum for no more than 24 h and then released at their capture location. All experimental procedures were approved by the national bioethical committee (Ministry for health, protocol n. 618/2020-PR), ISPRA - Institute for environmental protection and research, (protocol n. 13486 del 23/3/2020) and trapping and handling of animals were authorized by the Gran Paradiso National Park (protocol n. 0003037/2020 del 18/08/2020).

Behavioural trials

To estimate the level of boldness in different species we measured the escape behaviour and the mobility of animals in arena test [38]. The novel environment presented by the arena test provides a standardized procedure for comparing similar behaviour among species and populations [39]. Experiments were conducted during the active phase of the species daily activity cycles (around 10:30 pm). First, an animal was transferred from its cage into a bottom-less cylinder placed in the center of the arena, to accommodate it to for 1 min before the experiment started. The arena was made up with a wood box (100×100×100 cm), surrounded by four red light lamps to illuminate the arena without affecting the animal's behaviour (see Appendix A1 for description of the arena). After gently removing the cylinder, the animal was recorded for 600 seconds using a camera (Panasonic Lumix DMC-FT30EG-A) fixed above the arena. After the trial, the animal was recovered, placed into its cage and the arena cleaned with 75% alcohol [40]. Mobility and escape behaviour were assessed from animals tracks of recorded videos, using the software EthoVision XT 14.0 [41], measuring the total travelled distance in centimeters [42], and the latency to first jump in seconds, as an attempt to leave the arena by jumping over the edge of the walls [43]. Animals that travelled longer distances and showed a shorter latency time were considered bolder [44].

Statistical analyses

To evaluate the effect of elevation on behaviour, in two separate analyses for the escape behaviour and distance travelled, we used Bayesian generalized linear modelling. For the escape behaviour (latency time) as some animals had not moved during trials, we used a zero-altered Gamma distribution. Zero-altered (Hurdle) models, differently from zero-inflated models, quantify separately the probability that the response is zero or other non-zero value [45]. For the mobility (distance travelled) based on a preliminary analysis, we used a Gamma distribution with a log link function. Both analyses included elevation as continuous predictor, and sex and species as fixed factors. To test differential responses to elevation among species we tested the effect of elevation by species interactions. Model selection procedure was based on a stepwise backward approach and leave-one-out cross validation [46]. To improve model regularization, we adopted moderately informative prior distributions for regression slopes, with a normal distribution and mean of 0 and variance of 2 [47]. Parameter estimation was based on Markov Chains Monte Carlo methods with 4 chains, 5,000 iterations and a burn-in of 2,000 iterations. We used the Gelman-Rubin statistics and graphical inspection of posterior distributions of model parameters to check for convergence. Finally, we explored model residuals to detect the non-linearity of covariates and used posterior predictive checks to test for the goodness of fit of our data to the model. To measure the inter-specific variability in the latency time and the distance travelled we calculated the coefficients of variation (CV) for each species using the "var ()" function in R (package "cmvnorm")[48]. Statistical analyses were conducted in R [49] and STAN

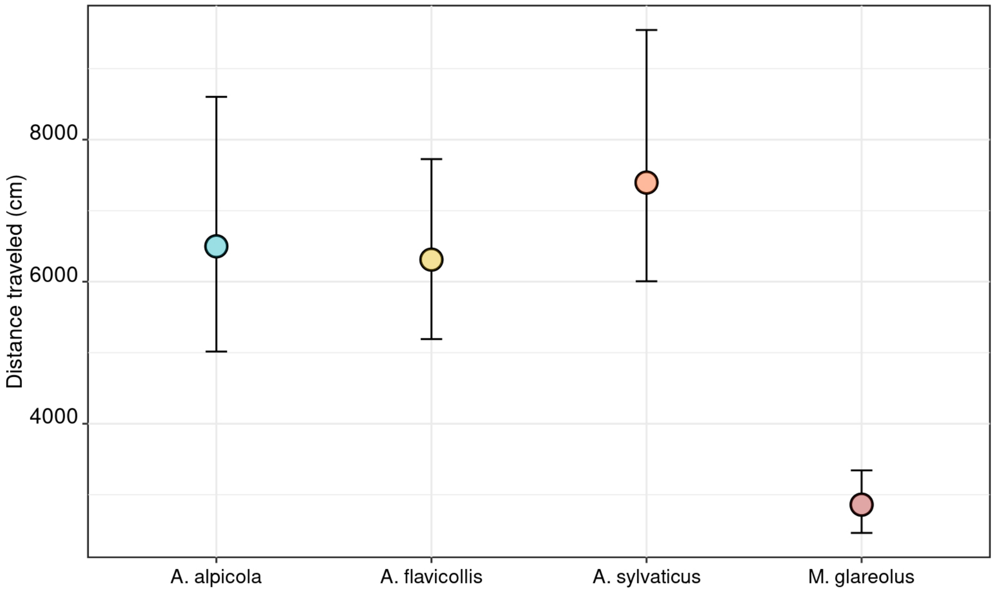

Figure 2: Conditional effect, showing interspecific differences in the distance travelled by individuals during the arena test.

Results

Behavioural experiments were conducted on 242 individuals (124 females and 118 males): 136 *Apodemus* spp. and 106 to *C. glareolus* (57 females and 49 males). After genotyping *Apodemus* spp. were determined as: 60 *A. flavicollis* (36 females and 24 males), 43 *A. sylvaticus* (10 females and 33 males) and 33 *A. alpicola* (21 females and 12 males). We found a negative correlation between latency time (before zero-transformation) and mobility (r = - 0.53).

Leave-one-out cross validation did not detect any effect of elevation, neither on the distance travelled, nor on the latency time to the first jump. Moreover, it did not detect any difference in these two quantities, between the two sexes (Table 1). As for species-specific differences, *C. glareolus* travelled smaller distances (mean ± SE= 2854.6 ± 267.7 cm) than species from the genus *Apodemus*: *A. flavicollis* = 6258.3 ± 390.9; *A. sylvaticus* = 6321 ± 411.7; *A. alpicola* = 6441.9 ± 423.6 cm (Fig. 2). Moreover, although individuals of *C. glareolus* did not have longer latency times than individuals from the genus *Apodemus*, model selection indicated that the zero-inflation parameter varied between species (Table 1). This was in line with the fact that 46.2% of *C. glareolus* did not jump during the experiment, while only about 11% of *Apodemus* did so (Fig. 3).

Finally, we found a significant difference between the species in the variance of the latency time, higher in *M. glareolus* (var ± SD = 60811.92 ± 246.6) and lower and almost similar for *A. flavicollis* (38371.82 ± 195.9), *A. sylvaticus* (33843.48 ± 183.9) and *A. alpicola* (20524.22 ± 143.2; Fig. 4). For the distance travelled we did not find any significant difference between the species in the variance of the data (p = 0.35).

Discussion

In this study, through a full controlled experiment, we explored the link between the altitudinal distribution of four sympatric wild rodent species and their behavioural characteristics, to highlight the role of the Alpine environment and its peculiar elevational gradient in shaping rodents' communities.

We measured two target behaviors in bank voles and *Apodemus* mice and found significant differences between these two groups. Our assumption that animals travelling longer distances and showing shorter latency time were bolder [44][52][53], was confirmed by the result where the latency to the first jump and the distance travelled were negatively correlated. We found evidence that different species can exhibit a specific behavioural type. For example, C. glareolus turned out to be a shy species, as it was more likely that animals did not jump at all when placed in a novel arena. In support of this finding, a study by Galsworthy et al. [54] highlighted the freezing behaviour of *C. glareolus* during manipulation and arena tests. The distance travelled by this species was much shorter than in *Apodemus* spp., confirming the limited mobility attitude and, therefore, perhaps shyness trait of *C. glareolus*. On the contrary, high level of boldness were previously described in *A. sylvaticus* [18], and in this study we confirmed that high mobility and rapid reaction to new environment, two manifestations of boldness, are also present in other *Apodemus* mice, such as *A. flavicollis* and *A. alpicola*.

Contrary to hypothesis H_3, no significant differences in the level of boldness were found between males and females, as instead reported in other studies [34][55]. In fact, in mammals risk-taking behaviors are often more beneficial for males than females. Males have relatively lower level of parental investment and must compete between each other for mating, thus potentially they can produce numerous offspring [56][57]. Females, on the other hand, face less intense competition for mating but are more limited in the number of potential offspring [12][58]. However, sex differences in risky behaviour appear highly species- and context- specific [59][60][61]. In rodents, behavioural tests on sex-related differences in risk taking and exploration brought mixed results [57][62][63][64][65]. This variation precludes broad empirical generalizations about the link between sex and risk taking. Clearly, a new predictive framework is needed for to explain and organize these differences.

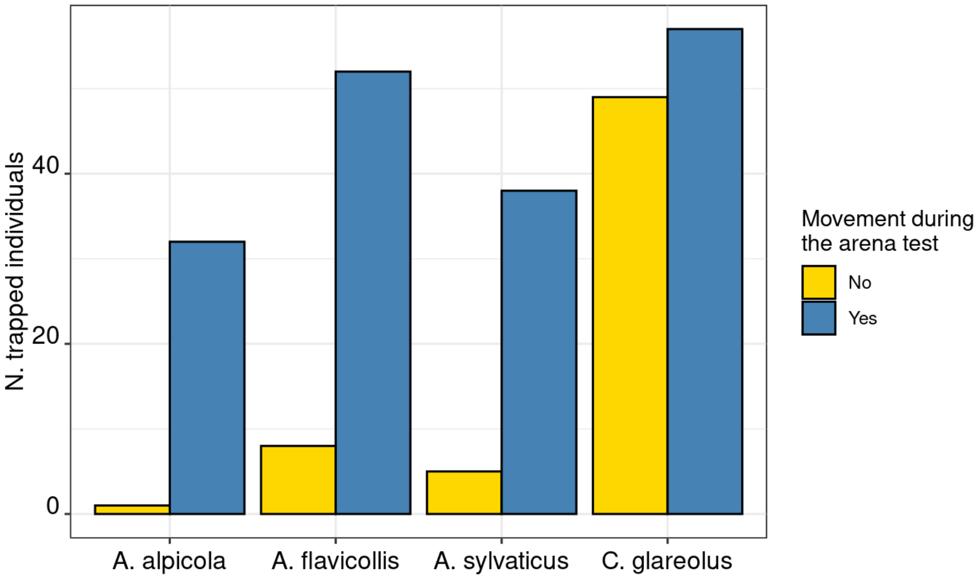

Figure 3: Number of trapped individuals, that did not move at all, during the arena test, between the four species.

We found a high variance of the escape behaviour (measured as latency time) in *C. glareolus*, confirming our hypothesis (H_2) that generalists species adapted to different microhabitat and to use different type of food resources, have a greater plasticity to adjust their behaviors, compared to other species, such as *A. flavicollis*, which are more specialists on diet (granivorous) and tend to perform well in a few habitat types, associated mostly with mature deciduous forests [19][66][67]. *C. glareolus* can be found in a wide range of habitats, such as deciduous, mixed and coniferous forests, and especially in summer season due to lack of resources, occasionally it can also be found in open or rocky areas, as long as there is shrub cover, actively avoiding food competition with the more aggressive *Apodemus* mice [32][68]. On the contrary, *Apodemus* spp. are more habitat selective. Although occasionally found in coniferous forests, *A. flavicollis* is a species related mostly to mature broad-leaved and mixed forests. It is mainly associated with forest edges [32], where it lives in sympathy with *A. sylvaticus* [69] sharing the same ecological niches. At high altitude, *A. alpicola* prefers green alder *Alnus viridis* shrubs and open environments characterized by herbaceous patches, rocky debris and low woody vegetation. In all these habitat *Apodemus spp.* lives in sympatry with *C. glareolus*, leading to a differential use of the microhabitats by these rodents [32]. This segregation is predicted to reduce interspecific competition, especially in favor of *C. glareolus* to avoid the more aggressive and bigger *Apodemus* spp. [70]. This differentiation of the spatial, trophic and temporal niche between the two taxa may have led to differences in behavioural traits [71].

Contrary to our prior expectation, elevation did not affect the latency time, nor the distance travelled by the four species (H_1). Species-specific behaviors are almost always influenced by social interactions and environmental conditions. The apparent absence of any influence of elevation on the behaviors here considered, could indicate a possible presence of a genetic up-regulation of behaviour expression in such species [72][73][74]. In fact, evidence suggests that about 50% of the variance in behavioural traits are explained by environmental factors [75] while phenotypic structure of behaviors closely resembles the underlying genetic architecture. The genetic basis of behavioural trait is complex: some genes influence a single trait while others influence multiple phenotypically distinct but covarying traits [76].

We are aware that considering only two behaviors to describe the degree of boldness in the analyses is a limitation of the study. Integrate the analysis of behaviors associated with the boldness continuum, such as latency to emerge from the trap [77] and response to manipulation [78], together with other behavioural traits, such as individuals' activity in a non-risky and a non-novel environment [16], could give greater support to the hypotheses presented here. Moreover, the recent advent of micro-sized GPS loggers [79], could allow to collect movement data, and to integrate differences in movement patterns with outcomes of behavioural experiments, obtaining more complex metrics of animal behaviour.

A comprehension of the behavioural adaptation could become even more critical considering climate change scenarios where the increasing temperatures, especially at high altitudes, are expected to cause species range shift and new species interactions [80]. Integrative studies on the genetic and physiological mechanisms underlying species behaviour, their selective benefits and microhabitat use will help to clarify how rodents have adapted to their environments. This will shed light on the adaptation of mountain species to this peculiar and extreme habitat.

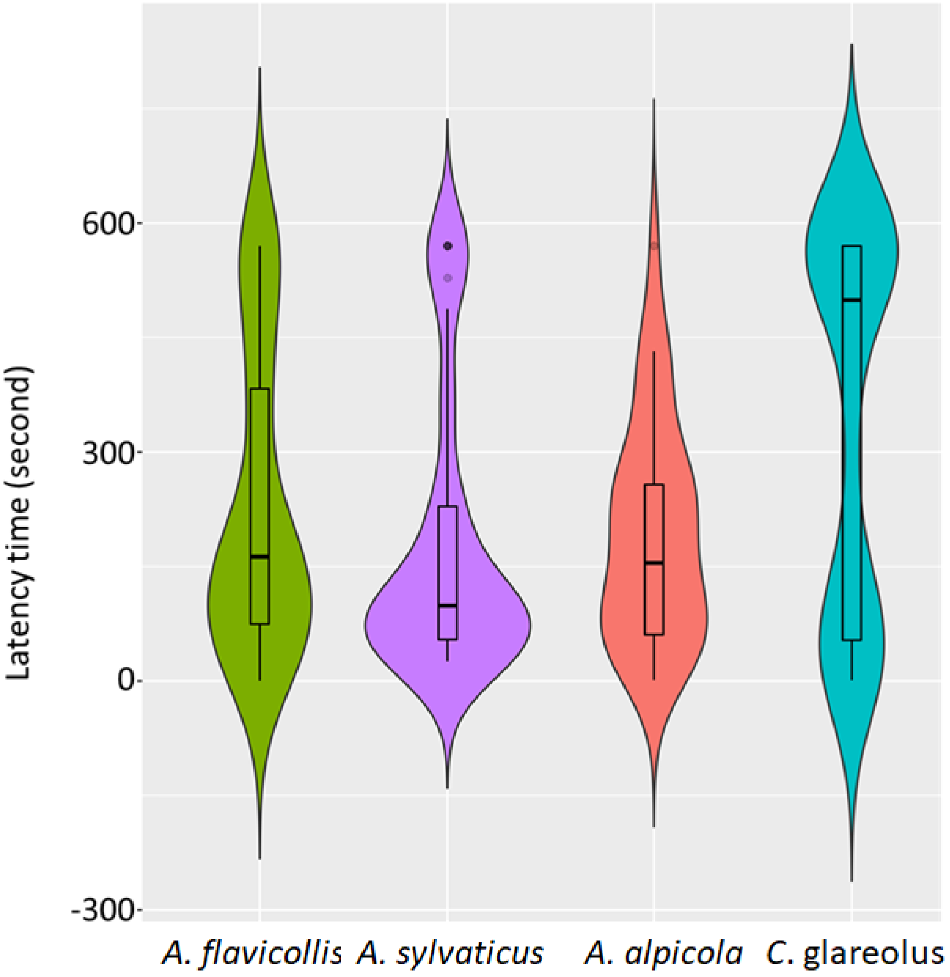

Figure 4: Violin boxplot of the variance coefficient of the latency time in the four species.

Table1. Overview of model selection, for the distance travelled and latency times, through Bayesian leave-one-out cross validation. The table represents model formula and the expected log-pointwise predictive density (ELPD, the closer to zero the better). For latency times, zero values correspond to odds ratio of the Hurdle gamma, representing the probability that values were zero. As the four species were treated as a factor variable with sum-to-zero contrasts, differences in the hu parameter are not directly interpretable from a table. But the model where zero-inflation varied by species was retained by cross validation. For a graphical interpretation, we encourage you to read Fig. 3, where the number of animals that did not jump was reported for each species. A null model is added for comparison for both measures.

Distance travelled	
Formula	**ELPD ± S.E.**
Distance elevation + species + sex + (elevation X species)	2265.0 ± 13.6
Distance elevation + species + (elevation X species)	-2264.3 ± 13.7
Distance elevation + species	-2263.5 ± 12.9
Distance species	-2262.6 ± 12.6
Distance 1	-2287.7 ± 9.7
Latency times	
Formula	**ELPD ± S.E.**
Non-zero values elevation + species + sex + (elevation X species) ∣ Zero values elevation + species	-1209.7 ± 38.6
Non-zero values elevation + species + sex + (elevation X species) ∣ Zero values species	-1209.0 ± 38.7
Non-zero values elevation + species + sex + (elevation X species) ∣ Zero values 1	-1226.8 ± 37.0
Non-zero values elevation + species + (elevation X species) ∣ Zero values species	-1207.8 ± 38.6
Non-zero values elevation + species ∣ Zero values species	-1206.6 ± 38.5
Non-zero values species ∣ Zero values species	-1205.9 ± 38.5

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Data availability statement

The reproducible dataset and software code is available at: `https://osf.io/ndmve/`

Conflict of Interest

The authors declared no conflict of interest.

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