Do exploration and risk-taking behaviors covary with metabolism and performance in an Asian agamid lizard (*Phrynocephalus vlangalii*)?

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Abstract

Ecological factors related to predation risks and foraging play major roles in determining which behavioral traits may mediate life history trade-offs and, ~~thus~~ therefore, the pace-of-life syndrome structure among behavioral, physiological and life-history traits. It has been proposed that activity/exploration or risk-taking behaviors are more likely to impact resource acquisition for organisms (individuals, populations, and species) foraging on clumped and ephemeral food sources than for organisms foraging on abundant and evenly distributed resources. In contrast, vigilance or freezing behavior would be expected to covary with the pace of life when organisms rely on food items requiring long bouts of handling. Nevertheless, it remains unclear how general this pattern. ~~In the present study, w~~We tested this hypothesis by examining the associations between exploration/risk-taking behaviors and metabolic/performance traits for the viviparous agamid lizard, *Phrynocephalus vlangalii*. This species forages on sparse and patchy food sources. The results showed positive correlations between exploration and endurance capacity, and between bite force and risk-taking willingness. Our current findings, in conjunction with our previous ~~(study~~work that showed~~ing~~ no correlations between freezing behavior and performance in this species~~ (Qi et al. 2014))~~, support the idea that behaviors in life-history trade-offs are natural history-dependent in *P. vlangalii*, and provide evidence that behavioral types play functional roles in life history trade-offs to supporting pace-of-life syndrome hypothesis.

Introduction

Phenotypic integration or correlation can result from evolutionary constraints, under which multiple traits are functionally connected such that no trait may respond independently to natural selection (Ingleby et al. 2013). Theorists have proposed that life-history characteristics and suites of physiological (metabolic, immunological and endocrine) traits may coevolve as a function of species- or population-specific environmental conditions forming a pace-of-life syndrome (POLS) (Ricklefs & Wikelski 2002). More recently, repeatable differences in behavior (i.e. “animal personality”) and performance traits have been integrated in POLS research (Careau et al. 2008; Wolf et al. 2007). Accordingly, it has been hypothesized that high activity, superficial exploration, and risk-taking willingness are positively correlated with locomotor performance and fighting ability (Careau & Garland Jr 2012). This prediction is based on the rationale that individuals with faster pace-of-life must perform better during foraging and territorial defense to satisfy the energetic demands of their behavioral strategy (Farwell & McLaughlin 2009; Garland 1999). Nevertheless, the results obtained from empirical studies on the links between metabolism/performance and behaviors have been mixed (Mathot et al. 2013; Royauté et al. 2015).

It is possible that mixed results in this field occurred because the researchers did not properly choose the behavioral type~~, insofar the~~: behavioral traits theoretically likely to be associated with the pace of life are determined by the type of resources an organism acquires and the foraging behavior of its predators (Dronne et al. 1999; Faure et al. 1998; Holt & Van Look 2004). For example, a~~A~~ctivity/exploration or risk-taking behaviors are more likely to impact resource acquisition in organism (individuals, populations, or species) foraging on clumped and ephemeral food sources than ~~would be the case for organisms~~those foraging on abundant and homogeneously-~~-~~distributed resources. Vigilance or freezing behavior ~~is~~ are instead more likely to covary with the pace of life when organisms rely on food items requiring long bouts of handling (Dronne et al. 1999). Thus far, however, the natural history-dependent behavior-metabolism/performance co-adaptations have rarely been investigated.

The Qinhai Toad-headed agama, *Phrynocephalus vlangalii*, is a small viviparous lizard living in northwestern China (Zhao 1999). They usually forage in open spaces in arid or semiarid regions covered by sparse and patchy vegetation in the Qinghai-Tibetan Plateau (Qi et al. 2012). The high-elevation individuals of *P. vlangalii* grow faster than the low-elevation ones (Caissard et al. 1996), consistent with higher potential food availability and higher active body temperatures at the higher altitude (Medou et al. 1997). Therefore, based on the rationale of natural history-dependent behavior-metabolism/performance coadaptation (Dronne et al. 1999), we hypothesized that exploration/risk-taking behavior, but not vigilance or freezing behavior, should coevolve with pace of life traits (metabolism and performance) in *P. vlangalii*. Our previous studies have demonstrated that freezing behavior did not correlate with locomotor performance (maximal endurance and sprint speed), consistent with this hypothesis (Peters et al. 2016; Qi et al. 2012; Qi et al. 2014). In the present study, we ~~further~~ examine the association between exploration propensity/risk-taking and metabolic rate/performance traits in male *P. vlangalii*, to further test our hypothesis.

Commented [HL1]: Do you mean individuals of the same species living at lower elevation or individuals of a different species that live at lower elevation? If the former, I suggest you write this sentence as "*P. vlangalii* that live at high elevation grow faster than individuals of the same species living at lower elevation (Caissard et al. 1996), consistent with higher potential food availability and higher active body temperatures at the higher altitude (Medou et al. 1997)." If the latter, you should provide the same of the species.

Commented [HL2]: I agree with the reviewers that presenting the metabolism information about this study aim is awkward. I suggest you end your Introduction with this sentence and then move the metabolism information further up into your introduction and/or into your methods.

Minimum metabolic rate (standard metabolic rate (SMR) for endotherm in the thermal neutral zone, basal metabolic rate for ectotherm at a specified ambient temperature) represents the maintenance costs from metabolically active organs such as gut, intestines and liver (Biro & Stamps 2010). These maintenance costs may profoundly affect individuals' behaviors. Individuals with a higher metabolic rate could potentially afford a faster pace of life, because a higher metabolic rate allows them to mobilize the energy needed to express a high level of activity, a fast exploration, or high levels of aggressiveness. Minimum metabolic rate can be also considered as "competitor" because it monopolizes energy that would otherwise available for other energy-demanding activities (Biro & Stamps 2010; Careau et al. 2008). For these reasons, we used standard metabolic rate (SMR) as a proxy for energy metabolism to test the coadaptation hypothesis.

Materials & methods

Animal sampling

All lizards were adult males (average SVL = 66.58 ± 5.68 mm, N = 47) from the Zoige Wetland Nature Reserve, in southwestern China (Qi et al. 2012). The subjects were caught by hand or in pitfall traps in early July 2015. After capture, all lizards were transferred to the Xiaman Conservation Station. A total of 13 individuals were captured from site A (latitude, 33°42’57.7” N; longitude, 102°29’23.4” E; altitude, 3471 m a.s.l.), and another 34 individuals were obtained from site B (latitude, 33°44’31.5” N; longitude, 102°30’15.9” E; altitude, 3454 m a.s.l.). At both sites, the sandy substrate is simiar~~The sand substrate is similar in both sites except for~~ but the vegetation density varies across sites. The vegetation is predominantly composed of *Dracocephalum heterophyllum* and *Carex aridula*, occasionally accompanied with *Astagalus sutchenensis*, *Anaphalis lacteal*, *Vicia cracca*, *Morina kokonorica*, *Oxytropsis glabra*, *Linum stelleroides* and *Clematis tangutica*. Captured lizards were individually housed in ~~card~~cardboard~~-~~ boxes (40L × 30W × 20H cm) with sand substrate from the field. Water and mealworms were provided *ad libitum*. To ~~make the captured lizards experience the environmental conditions as wild lizards would~~approximate conditions in the field, we moved the ~~carton~~ boxed outside and basked ~~all~~ the lizards when the weather allowed. All animal procedures in this study were carried out in accordance with and approved by the Animal Care and Use Committee at the Chengdu Institute of Biology, Chinese Academy of Sciences (20151220) and the field experiments were approved by the Management Office of the Zoige Nature Reserve (20150701).

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Commented [HL4]: Where were the lizards housed once you captured them? At the Chengdu Institute of Biology?

Morphology and performance measurement

As we wished to evaluate how body size covaries with behavioral, metabolic and performance traits, ~~W~~we measured the snout-vent length (SVL), to the nearest mm, and body mass, to the nearest mg, of each lizard~~to see how body size covaries with behavioral, metabolic and performance traits~~. Each lizard was marked with ~~an~~ acrylic paint on the dorsum to facilitate identification.

Due to the close link between performance and temperature in ectothermic species

(Qi et al. 2014), we standardized ~~the measurement condition by~~ temperature ~~control~~during physical testing. First, the subjects' bite force was measured at room temperature (15°C) by inducing each lizard to bite the free end of a steel bite-plate connected to an isometric force transducer (S1-100NHL, 0~100N, Nanjing Bio-inspired Intelligent Technology Co. Ltd.). Bite forces were measured three times per individual, and the maximum value was used in further analysis (Lailvaux et al. 2012). Second, the subjects were warmed with an infrared heater before measuring endurance and sprint speed in order to insure the lizards were active and to standardize body temperature (22~35^{o}C). Detailed protocols for measuring sprint speed and endurance have been described previously (Qi et al. 2014). Briefly, lizards were stimulated to run by tapping the base of the tail with a paintbrush (Noble et al. 2014). All runs were recorded using a camera (Panasonic, HDC-HS60) and sprint speed was calculated as the fastest speed along a 1.5-m racetrack. To ensure that the lizards experienced environmental conditions similar to those in the wild, the racetrack was covered with sand from the field. Endurance was ~~then~~ measured immediately following after sprint speed tests. Lizards were placed in a circular racetrack and stimulated to run by tapping the base of the tail using a paintbrush. We considered the subject as exhausted if the lizard did not run after tapping the tail ten times. Total movement time before exhaustion was regarded as a proxy of endurance. Sprint speed and endurance were measured once per day over two consecutive days. We used the maximum value for subsequent analyses, because lizard performance can be highly variable due to differences in motivation and other factors (Losos et al. 2002).

Personality measurement

Two behavioral traits, exploration and risk-taking, were measured and used as proxies of the lizards' personalities. Similar traits have been measured in many lizard species and have been shown to be consistent across different contexts (Cote & Clobert 2007; Lopez et al. 2005; Stapley & Keogh 2004).

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Additionally, what order did you run the performance assessments, personality assessments, and metabolic assessments in? Or, again, were these counterbalanced across subjects? Please provide this information.

Finally, how long had the subjects been in the lab (i.e. how long did you keep them after capturing them from the wild) before you began running these assessments?

Exploration: Lizards were individually introduced into a novel enclosure (60L ×44W

×37H cm) and were initially placed ~~initially~~ in an opaque ~~masking non-transparent~~ plastic box in the center of the enclosure (Fig. 1a). Two PVC refuge burrows (10L ×4R cm) were set at each end of the enclosure; these served as the goal of lizard exploration. After a two minute~~s~~ ~~of~~ acclimation period, the plastic box was lifted, exposing the lizard to the novel enclosure. ~~and the trial was run for~~Over 20 minutes~~. W~~ we scored the following aspects of the subject's behavior: (i) time in locomotion (exploration intensity I) and (ii) ~~time~~ latency to enter each of the two PVC refuge burrows in the enclosure~~s~~ (exploration intensity II). The time to enter refuges was taken as measurement of quickness to explore a novel environment, and time in locomotion was taken as a measurement of exploration intensity.

Risk-taking: ~~r~~Risk-taking is the propensity to take risks, especially in novel situations, and is usually measured experimentally in relation to anti-predatory behavior or individual responses to novel cues. In this study, we assayed risk-taking in an anti-predatory context. The trial was carried out in the same enclosure as the exploratory assay, however the refuge arrangement was different. We randomly assigned one of the two PVC burrows as a basking site by suspending a 25W incandescent bulb (special heat bulb for reptiles) ca 15 cm above at the burrow entrance, while the other PVC burrow was made cold by surrounding it with ice (Fig. 1b). As for the test of exploration, ~~T~~the lizards ~~was~~ were introduced into the enclosure ~~under~~ in the ~~masking~~ opaque plastic box, and allowed two minutes for acclimation. Once the trial began, we removed the plastic box and allowed lizards 15 minutes to ~~reach~~ discover the basking burrow. We then simulated a predatory attack by chasing each lizard off the basking refuge until it entered the cold burrow. The time it took for the lizards to ~~then~~ return to the~~ir~~ basking site~~s~~ (i.e. ~~R~~risk-taking intensity) was measured ~~and used~~ as a proxy of lizard risk-taking. Thus, a higher intensity index means lower risk-taking willingness.

Metabolic capacity measurement

The oxygen volume consumed by animals provides a convenient and readily measured estimate of their metabolic rates. We measured lizard oxygen consumption using an open air flow respirometer from TSE Systems (Bad Homburg, Germany) comprised of a source of pressurized gas (14% O_2, 86% N_2, this oxygen pressure is equal to the oxygen concentration at their habitats), Low Pressure Regulator G261, 8 Channel Gas Switcher G244, Sample Chambers, 8 Channel Gas Flow Controller and Monitor G246, Differential Oxygen Analyzer S104 and CO_2 analyzer S157 with Gas Pump P651. After two days' fasting, the lizard was placed individually in a 190-mL darkened chamber. To standardize the measuring condition, we controlled the airflow at 110 mL m1/min and set the temperature at 25 ± 0.5°C. Oxygen concentration was measured for 300s ~~per~~ every hour ~~over~~ for a period of six hours~~' period~~, and the animals were weighed after each of the six measurements. We calculated the oxygen consumption as the difference between the oxygen concentration in the ambient air and at the chamber exit. The equation was follows: ~~VO_2=FR*(F_iO_2-F_eO_2) - (F_eO_2*VCO_2)/1-F_eO_2.~~

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Commented [HL7]: Is this what you mean? Or simply that they were weighed once at the end of the six hours?

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$$VO_2 = \frac{FR * ((F_1O_2 - F_eO_2) - (F_eO_2 * VCO_2))}{1 - F_eO_2}$$

$$VO_2 = (FR * (F_1O_2 - F_eO_2)) - \frac{(F_eO_2 * VCO_2))}{1 - F_eO_2}$$

Where FR is the flow rate, F_iO_2 and F_eO_2 are the fractional concentration of O_2 entering and exiting the respirometry chamber, respectively, and VCO_2 is the rate of CO_2 production. The minimum consumption based on six time points was used to calculate the standard metabolic rate (SMR) (mL O_2/ h).

Statistical Analyses

All data were analyzed using R software version 3.2.2 (R-Core-Team 2013) and SPSS 19.0 (International Business Machines Corporation). Five ~~individuals~~ of the 47 lizards were excluded from further analyses, because they were highly active and did not meet the SMR measurement assumption (Kristín & Gvoždík 2012). A high proportion (33/42) of the remaining lizards did ~~not~~ never entered either of the two refuges during the exploration test. For this reason, we regarded the TER as a binomial

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variable, with lizards that entered~~ing~~ the refuge assigned as "1", and lizards that did not enter~~ing~~ assigned as "0". Similarly, a high proportion (25/42) of the lizards did not return to the basking site during the risk-taking test after the simulated predator attack. For this reason we regarded risk-taking intensity as a binomial variable, with lizards that returned~~ing~~ to the basking site assigned as "1", and lizards that did not return~~ing~~ to the basking site assigned as "0".

All continuous variables were normalized (RMR and endurance were log-transformed and exploration intensity I was square root-transformed) and standardized (mean=0, SD=1) to facilitate the following analyses.

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We used the residual of the regression of performance against body temperature if we detected any significant correlation between them. We examined the correlations among behavioral traits (exploration and risk-taking), body size (body mass and SVL), metabolic rate and performances (sprint speed, endurance, and bite force) to verify the relationship between behavior, physiology and performance predicted by the POLS. For the correlation analyses between exploration intensity II (i.e. latency to enter the burrows), risk-taking intensity and the other variables, we used Spearman correlations since these variables are binominal. For the correlation tests between continuous variables, Pearson's produce-moment correlations were applied. If performance traits were significantly affected by body size (e.g. bite force), we used the residuals of the observed variable against SVL for the correlation test. All means are reported as mean ± 1 SE.

Results

We found that our two measures of exploration intensity ~~I was~~were negatively correlated ~~with exploration intensity II~~ but we found no association ~~was detected~~ between risk-taking intensity and either of our two exploration intensity indexes (Table 1).

The lizards' performance measurements were not correlated with temperature (sprint speed: r=0.15, $P = 0.35$; endurance: r = 0.11, $P = 0.49$; bite force: r = 0.07, $P = 0.67$). So, we used the original performance trait data for the following analysis. There was

Commented [HL11]: I am not sure what you mean by this – please clarify no significant association between performance traits (bite force, sprint speed, endurance ability) and SMR, and among the performance traits (Table 1).

Endurance ability, but no other performance measurement~~s~~, was correlated with our first measure of exploration (i.e. exploration intensity I) ($P < 0.05$) (Table 1, Fig. 2). Moreover, only bite force/residual bite force was correlated with risk-taking intensity ($P < 0.05$). In addition, body mass was marginally correlated with risk-taking intensity ($P = 0.05$).

Discussion

In this study, we found positive correlations between exploration and endurance capacity, and between risk-taking willingness and bite force. Similar associations have been reported in *Zootoca vivipara*, and *Tupinambis merianae* (Herrel et al. 2009). Therefore, ~~the~~ our results support our hypothesis that the coadaptation pattern is behavioral type-dependent ~~and imply~~which implies that the role of behaviors mediating life history trade-offs is associated with the natural history of the species.

Bite force variation among ~~individuals~~ vertebrates has been found to correlate with measures related to fitness, including energy intake efficiency when foraging, number and quality of mates acquired, or anti-predation capacity (Anderson et al. 2008). Therefore, bolder individuals with greater bite force may support a faster pace-of-life to maximize fitness payoffs. Androgens, such as testosterone, may mediate the positive correlation between risk-taking willingness and bite force, since androgens can indirectly affect performance by modifying growth rates and organizing the development of morphological traits as well as mediate plastic changes in behavior and morphology (Diemer et al. 1999; Noble et al. 2014).

Endurance capacity mainly results from enzymatic, physiological and morphological muscle attributes, such as body size, tight-muscle mass and aerobic metabolic capacity (Garland 1984). Because we found no correlation between body size (SVL or body mass) with endurance ability in *P. vlangalii*, the association between exploration intensity and endurance ability seems more likely mediated by its association with metabolic capacity. A recent study reporting that maximal oxygen consumption/metabolic scope constrain individual behavioral variation supports this idea (Elias et al. 2010). It is also worth noting that body mass but not the SVL of male *P. vangalii* is marginally correlated with risk-taking intensity, suggesting individuals with better body conditions are willing to take more risk during foraging or mate searching since they are less vulnerable to predation (Bussiere et al. 2008). Similar correlations have been shown in other vertebrates (Polak & Starmer 2005; Roulin et al. 2008).

~~The~~ Our data show that exploration was positively correlated with endurance capacity in *P. vangalii*, however, SMR and exploration we~~a~~re not associated. This is surprising insofar as that locomotor performances represent correlates of maximal anaerobic (e.g. sprint speed) or aerobic capacity (e.g. endurance capacity) (Arnegard et al. 2010), and SMR is highly correlated with maximum oxygen consumption in general (Vergara et al. 2012). Notably, another study found the sprint speed of garden skinks *Lampropholis delicata* was not correlated with RMR (Merritt et al. 2013). A variety of evidence indicates that reptiles reply heavily upon anaerobic metabolism (Bennett & Gleeson 1979).~~ Hence a~~Additional studies directly examining the association between anaerobic glycolysis (e.g. lactate) and behavioral/performance traits may reveal the potential linkages. In addition to these theoretical considerations, other experimental factors may have weakened the associations obtained between metabolism and behavioral/performance traits, including low statistical power due to lack repeatable measurement in our design, or sample reduction (the 5 individuals potentially indicating a consistent phenotype).

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Conclusions

Overall, ~~this~~ our study aimed to test the hypothesis if that natural history (distribution pattern of food resource) specific behaviors-pace of life integration exists in *P. vlangalii*. Our results support the idea that in this species exploration/risk-taking behavior rather than freezing behavior are more important mediators of the life-history tradeoff. Further work to test the POLS may benefit from considering the role of the species' natural history in coadaptation among behavior, physiology, and life history (Dronne et al. 1999;

Holt & Van Look 2004).

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Reference

Anderson RA, McBrayer LD, and Herrel A. 2008. Bite force in vertebrates: opportunities and caveats for use of a nonpareil whole-animal performance measure. *Biological Journal of the Linnean Society* 93:709-720. DOI 10.1111/j.1095-8312.2007.00905.x

Arnegard ME, McIntyre PB, Harmon LJ, Zelditch ML, Crampton WGR, Davis JK, Sullivan JP, Lavoue S, and Hopkins CD. 2010. Sexual Signal Evolution Outpaces Ecological Divergence during Electric Fish Species Radiation. *American Naturalist* 176:335-356. 10.1086/655221

Bennett AF, and Gleeson TT. 1979. Metabolic Expenditure and the Cost of Foraging in the Lizard Cnemidophorus-Murinus. *Copeia*:573-577.

Biro PA, and Stamps JA. 2010. Do consistent individual differences in metabolic rate promote consistent individual differences in behavior? *Trends in ecology & evolution* 25:653-659. 10.1016/j.tree.2010.08.003

Bussiere LF, Hunt J, Stolting KN, Jennions MD, and Brooks R. 2008. Mate choice for genetic quality when environments vary: suggestions for empirical progress. *Genetica* 134:69-78. 10.1007/s10709-007-9220-z

Caissard JC, Faure O, Jullien F, Colson M, and Perrin A. 1996. Direct regeneration in vitro and transient GUS expression in Mentha x piperita. *Plant Cell Reports* 16:67-70.

Careau V, and Garland Jr T. 2012. Performance, personality, and energetics: correlation, causation, and mechanism. *Physiological and Biochemical Zoology* 85:543-571. 10.1086/666970

Careau V, Thomas D, Humphries MM, and Reale D. 2008. Energy metabolism and animal personality. *Oikos* 117:641-653. 10.1111/j.0030-1299.2008.16513.x

Cote J, and Clobert J. 2007. Social personalities influence natal dispersal in a lizard. *Proceedings of the Royal Society B-Biological Sciences* 274:383-390. 10.1098/rspb.2006.3734

Diemer F, Caissard JC, Moja S, and Jullien F. 1999. Agrobacterium tumefaciens-mediated transformation of Mentha spicata and Mentha arvensis. *Plant Cell Tissue and Organ Culture* 57:75-78. Doi 10.1023/A:1006280521212

Dronne S, Jullien F, Caissard JC, and Faure O. 1999. A simple and efficient method for in vitro shoot regeneration from leaves of lavandin (Lavandula x intermedia Emeric ex Loiseleur). *Plant Cell Reports* 18:429-433.

Elias DO, Mason AC, and Hebets EA. 2010. A signal-substrate match in the substrate-borne component of a multimodal courtship display. *Current Zoology* 56:370-378.

Farwell M, and McLaughlin RL. 2009. Alternative foraging tactics and risk taking in brook charr (Salvelinus fontinalis). *Behavioral Ecology* 20:913-921. 10.1093/beheco/arp059

Faure O, Diemer F, Moja S, and Jullien F. 1998. Mannitol and thidiazuron improve in vitro shoot regeneration from spearmint and peppermint leaf disks. *Plant Cell Tissue and Organ Culture* 52:209-212. Doi 10.1023/A:1006029123437

Garland T. 1984. Physiological Correlates of Locomotory Performance in a Lizard - an Allometric Approach. *American Journal of Physiology* 247:R806-R815.

Garland T. 1999. Laboratory endurance capacity predicts variation in field locomotor behaviour among lizard species. *Animal Behaviour* 58:77-83. DOI 10.1006/anbe.1999.1132

Herrel A, Andrade DV, de Carvalho JE, Brito A, Abe A, and Navas C. 2009. Aggressive Behavior and Performance in the Tegu Lizard Tupinambis merianae. *Physiological and Biochemical Zoology* 82:680-685. 10.1086/605935

Holt WV, and Van Look KJW. 2004. Concepts in sperm heterogeneity, sperm selection and sperm competition as biological foundations for laboratory tests of semen quality. *Reproduction* 127:527-535. 10.1530/rep.1.00134

Ingleby FC, Hunt J, and Hosken DJ. 2013. Heritability of male attractiveness persists despite evidence for unreliable sexual signals in Drosophila simulans. *Journal of evolutionary biology* 26:311-324. 10.1111/jeb.12045

Kristín P, and Gvoždík L. 2012. Influence of respirometry methods on intraspecific variation in standard metabolic rates in newts. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology* 163:147-151. 10.1016/j.cbpa.2012.05.201

Lailvaux SP, Gilbert RL, and Edwards JR. 2012. A performance-based cost to honest signalling in male green anole lizards (Anolis carolinensis). *Proceedings of the Royal Society B-Biological Sciences* 279:2841-2848. 10.1098/rspb.2011.2577

Lopez P, Hawlena D, Polo V, Amo L, and Martin J. 2005. Sources of individual shy-bold variations in antipredator behaviour of male Iberian rock lizards. *Animal Behaviour* 69:1-9. 10.1016/j.anbehav.2004.05.010

Losos JB, Creer DA, and Schulte Ii JA. 2002. Cautionary comments on the measurement of maximum locomotor capabilities. *Journal of Zoology* 258:57-61. 10.1017/S0952836902001206

Mathot KJ, Martin K, Kempenaers B, and Forstmeier W. 2013. Basal metabolic rate can evolve independently of morphological and behavioural traits. *Heredity* 111:175-181. 10.1038/hdy.2013.35

Medou G, Faure O, Jullien F, Colson M, and Perrin A. 1997. Caulogenesis and terpenic synthesis in vitro in peppermint. *Acta Botanica Gallica* 144:371-379.

Merritt L, Matthews PGD, and White CR. 2013. Performance correlates of resting metabolic rate in garden skinks Lampropholis delicata. *Journal of Comparative Physiology B-Biochemical Systemic and Environmental Physiology* 183:663-673. 10.1007/s00360-012-0736-x

Noble DWA, Fanson KV, and Whiting MJ. 2014. Sex, androgens, and whole-organism performance in an Australian lizard. *Biological Journal of the Linnean Society* 111:834-849. 10.1111/bij.12252

Peters RA, Ramos JA, Hernandez J, Wu YY, and Qi Y. 2016. Social context affects tail displays by Phrynocephalus vlangalii lizards from China. *Scientific Reports* 6. Artn 31573

10.1038/Srep31573

Polak M, and Starmer WT. 2005. Environmental origins of sexually selected variation and a critique of the fluctuating asymmetry-sexual selection hypothesis. *Evolution* 59:577-585.

Qi Y, Noble DW, Fu J, and Whiting MJ. 2012. Spatial and social organization in a burrow-dwelling lizard (Phrynocephalus vlangalii) from China. *PloS one* 7:e41130. 10.1371/journal.pone.0041130

Qi Y, Noble DW, Wu Y, and Whiting MJ. 2014. Sex-and performance-based escape behaviour in an Asian agamid lizard, Phrynocephalus vlangalii. *Behavioral Ecology and Sociobiology* 68:2035-2042. 10.1007/s00265-014-1809-5

Ricklefs RE, and Wikelski M. 2002. The physiology/life-history nexus. *Trends in ecology & evolution* 17:462-468. Pii S0169-5347(02)02578-8

Doi 10.1016/S0169-5347(02)02578-8

Roulin A, Gasparini J, Bize P, Ritschard M, and Richner H. 2008. Melanin-based colorations signal strategies to cope with poor and rich environments. *Behavioral Ecology and Sociobiology* 62:507-519. 10.1007/s00265-007-0475-2

Royauté R, Greenlee K, Baldwin M, and Dochtermann NA. 2015. Behaviour, metabolism and size: phenotypic modularity or integration in Acheta domesticus? *Animal Behaviour* 110:163-169. 10.1016/j.anbehav.2015.09.027

Stapley J, and Keogh JS. 2004. Exploratory and antipredator behaviours differ between territorial and nonterritorial male lizards. *Animal Behaviour* 68:841-846. DOI 10.1016/j.anbehav.2004.02.008

Vergara P, Martinez-Padilla J, Mougeot F, Leckie F, and Redpath SM. 2012. Environmental heterogeneity influences the reliability of secondary sexual traits as condition indicators. *Journal of evolutionary biology* 25:20-28. 10.1111/j.1420-9101.2011.02399.x

Wolf M, Van Doorn GS, Leimar O, and Weissing FJ. 2007. Life-history trade-offs favour the evolution of animal personalities. *Nature* 447:581-584. 10.1038/nature05835

Zhao K. 1999. Phrynocephalus kaup. *Fauna Sinica, Reptilia* 2:153-193.

Fig. 1 Schematic diagram of the apparatus used for personality measurement in the toad headed agama *Phrynocephalus vlangalii*. A) Exploration measurement. Lizards were initially set in an opaque box in the center. Two minutes later, the box was lifted and the trial was run for 20 minutes. Time in locomotion and time to enter either PVC refuge are counted as the intensity of exploration. B) Risk-taking measurement. A 25W incandescent bulb was suspended close to one side of PVC burrow as basking site, while the other PVC burrow was made cold by surrounding it with ice. The lizard was acclimated for 2 minutes under the masking box. Then the box was removed, and lizards were allowed to approach the basking site in 15 minutes. Then an experimenter chased each lizard off the basking refuge until they entered the cold burrow. The time to then return to their basking sites was used to evaluate the risk-taking level.

Fig. 2 The correlation between exploration intensity I and endurance capacity (a), risk-taking intensity and bite force (b) in the toad headed agama *Phrynocephalus vlangalii*. The dotted line represents 95% confidence intervals.