Original article

Do morphological condition indices predict locomotor performance in the lizard *Podarcis sicula*?

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ABSTRACT

Biologists have developed a number of simple metrics to assess the health and energetic status of individual organisms and populations. While these condition indices have been widely used to address questions in evolutionary ecology and conservation biology, the ability of such indices to predict ecologically relevant locomotor performance abilities remains unknown. We show here that the functional links between six commonly used morphological condition indices and locomotor performance in two populations of Adriatic lizards (*Podarcis sicula*) are weak at best. Indeed, no indices consistently predict either maximum sprint speed or maximum exertion across sexes, seasons or populations. These results cast doubt on the ecological relevance of morphological condition indices in terms of locomotor performance, measured in laboratory conditions, at least in this species. We urge caution in using condition indices as proxies for individual physiological or phenotypic quality in ecological and evolutionary studies.

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1. Introduction

Condition is considered to be a key concept in ecology and evolutionary biology. Broadly defined, condition is thought to encompass the general health and vigor of an organism. As such, it is commonly used as a proxy for phenotypic "quality" and has been linked in the past to variables such as reproductive success (Atkinson and Ramsay, 1995), immune response (Gleeson et al., 2005), and ultimately fitness (Svensson et al., 2002; but see Dibattista et al., 2007). Indeed, the view of condition as being fundamental to evolutionary processes has previously proved useful to our understanding of female preferences (e.g. Wagner and Hoback, 1999), male

ornamentation (e.g. Cotton et al., 2004), and sexual selection in general.

Despite this importance of condition to evolutionary ecology, there is surprisingly little consensus as to what comprises organismal condition. Condition is currently conceptualized as the acquired resources available for allocation to fitness-enhancing traits (Hunt et al., 2004; Tomkins et al., 2004). As such, it is most commonly estimated by one of several morphological "condition indices" (CIs) based on either residual body mass or some other combination of body mass and body size (Stevenson and Woods, 2006; but see Dahlhoff, 2004 for a discussion of biochemical indices). These indices supposedly correlate with individual nutritional

state or fat stores (e.g. Weatherhead and Brown, 1996); thus, individuals exhibiting high CIs are thought to be in positive energy balance, and hence have more acquired resources available for allocation to important ecological tasks. By contrast, individuals exhibiting low CIs are thought to be in negative energy balance (Jakob et al., 1996; Speakman, 2001). The use of condition indices is, however, controversial, as many indices are based on untested scaling assumptions, or otherwise subject to criticism on statistical grounds (Jakob et al., 1996; Kotiaho, 1999; Green, 2000). Despite these criticisms, CIs are still commonly used in ecological and evolutionary studies, and are also widely applied to conservation and monitoring programs (Stevenson and Woods, 2006; Amo et al., 2006, 2007).

In addition to statistical concerns over various condition indices, an unresolved question is whether *any* CIs convey any useful information on individual whole-organismal capacities that might impact on overall fitness. Indeed, the implicit assumption that individuals exhibiting high CIs are in some way more ecologically capable than those with poorer indices has seldom been rigorously tested, and while some studies support the ecological significance of condition indices (e.g. Murray, 2002; Ardia, 2005; Schulte-Hostedde et al., 2005), others show that the relationships between CIs and fitness/survival are generally weak and heterogeneous (e.g. Fisher et al., 2005; Dibattista et al., 2007). Given the widespread use of CIs in evolutionary ecology, as well as the assumed utility from a species management perspective, validation of the ecological relevance of such indices should be of high priority.

Previous studies have attempted to link locomotor performance with morphological or enzymatic correlates in various species (e.g. Gibb and Dickson, 2002; Odell et al., 2003), but none have rigorously tested the predictive value of several commonly used morphological condition indices in a single species. Here, we take a functional approach to evaluating condition indices by examining the relationship between condition (as estimated using six different morphological indices) and whole-organism performance (in this case, two kinds of locomotor performance, sprint speed and exertion) in a Mediterranean lizard species. Whole-organism performance capacities are considered ecologically relevant by definition (Huey and Stevenson, 1979; see also discussions by Irschick and Garland, 2001 and Lailvaux and Irschick, 2006), and locomotor performance in particular has been shown to be a valuable determinant of overall fitness in nature through effects on survival (e.g. O'Steen et al., 2002; Miles, 2004; Le Galliard et al., 2004; Husak, 2006) and/or reproductive success in many animal species (Peterson and Husak, 2006; Husak et al., 2006; Husak and Fox, 2006), as well as being linked to dispersal (e.g. Phillips et al., 2006). In addition to fitness effects, locomotor performance is an often-extreme activity, and hence sums the output of several physiological processes (Lailvaux and Irschick, 2006); indeed, the costs of locomotion accounts for a significant amount of daily energy expenditure in lizards (Christian et al., 1997). If morphological CIs are indeed useful indicators of phenotypic "quality", then one might predict that high individual performance capacity would be reflected in a high individual condition index. By contrast, individuals in poorer condition should achieve correspondingly poorer performance. We tested this prediction by measuring locomotor performance in two populations of the lizard *Podarcis sicula* from two different Adriatic islands, Pod Mrčaru and Pod Kopište, off the coast of Croatia. The Pod Mrčaru population was experimentally introduced in 1971 by Nevo et al. (1972), from the island of Pod Kopište. Genetic analysis confirmed that specimens on Pod Mrčaru and Pod Kopište both belong to *P. sicula* (Vervust et al., unpublished data), yet the two populations have been shown to differ considerably in performance, morphology, sexual size dimorphism and predation pressure (Vervust et al., 2007). Thus, this system provides an ideal opportunity to examine the predictive value of CIs in two different and isolated, yet proximate, populations within a single species.

We measured two kinds of performance (maximum speed and maximum exertion, an index of endurance) and calculated six commonly used reptile condition indices for each individual. Sprinting and endurance have been previously been shown to trade-off in lacertid lizards, including *P. sicula*, such that good sprinters exhibit poor stamina and vice-versa (Vanhooydonck et al., 2001). We therefore gave our hypothesis the maximum chance of support by examining two different aspects of performance, which are likely driven by different metabolic pathways, and hence represent different aspects of physiological or phenotypic "quality" (see Odell et al., 2003 for a similar approach). The six CIs measured comprise three ratio and three residual indices (Stevenson and Woods, 2006), including one morphological index particular to lizards, the residual diameter of the tail base. Because a useful index of condition should consistently predict performance within a species regardless of source population, sex, or season, we conducted these measurements on each island for males and females in both spring and fall. We then determined, using both linear and non-linear regression analyses, which condition indices (if any) significantly predicted maximum locomotor performance within each population, sex and season respectively. Finally, because condition might be expected to vary across seasons and populations as a function of food availability, predation pressure or differential energy expenditure during reproduction, we also compared variances of each index to determine if all CIs reflect changes in condition equally.

2. Methods

2.1. Study animal and system

During April and September 2006, we captured (by noosing) 308 and 312 respectively, adult *Podarcis sicula* (Rafinesque-Schmaltz, 1810) on two islets, Pod Mrčaru (42°46′N, 16°46′E) and Pod Kopište (42°45′N, 16°43′E). Lizards were individually stored in cloth bags and transported to the field station on the nearby island of Lastovo. The islets resemble each other in general aspect – both consist of organic limestone, are of comparable size, and have a central, vegetated zone (rising up to 20 m on Pod Mrčaru and 30 m on Pod Kopište), encircled by a more barren rocky belt.

The Italian wall lizard *Podarcis sicula* is a robust, ground-dwelling, diurnal, heliothermic, active foraging lacertid lizard

(adult snout-vent length [SVL] 55–70 mm) that occupies a variety of semi-open habitats in the Mediterranean. Adult males have larger heads, longer hind limbs and enlarged femoral pores than females. We analyzed only females, which were visible not pregnant. A review of the general biology of *P. sicula* can be found in Henle and Klaver (1986). Both performance traits are important to the daily lives of this species, such as predator escapement (Vervust et al., 2007) and feeding (Henle and Klaver, 1989). These lizards feed on insects and plants, which can be in short supply during summer time (Radovanović, 1956). During spring, insects and flowering plants are abundant and eaten by lizards (Herrel, unpublished data), whereas in the late summer vegetation is shriveled and insects are scarce.

2.2. Morphometrics and performance

Lizards were measured to the nearest 0.01 mm using electronic callipers (CD-20PP, Mitutoyo Corporation, Japan). Prior to each performance trial, lizards were placed for at least 1 h in large outdoor terraria wherein they could thermoregulate freely. Before each measurement, we ensured that the lizard's body temperature was within the optimal range for sprinting (~36 °C, Van Damme et al., 1990), using a thermocouple connected to an electronic thermometer (APPA 51, precision 0.1 °C). Maximal sprint speed was measured by chasing lizards three times along a horizontal 2 m racetrack with a cork substrate. The fastest time over any 25 cm interval (as recorded by photocells placed alongside the track) was considered an estimate of an individual's maximal sprint performance. We scored each trial as "good" or "bad" according to standard criteria (Tsuji et al., 1989). Only "good" trials were retained for analysis. Exertion was estimated by chasing lizards along a torus track (1 m diameter), until they reached exhaustion (Bennett, 1980). We considered lizards "exhausted" when they no longer responded to 10 consecutive (gentle) taps on the dorsum. The time elapsed between the start and the end of the run was taken as a measure of exertion. Upon completion of the measurements, and within 48 h of capture, the lizards were individually marked by toeclipping and released at the exact site of capture. Only lizards with intact tails were included in our analyses.

2.3. Condition indices

We estimated phenotypic condition in *P. sicula* using five morphological condition indices that have been generally applied to reptiles in the past (Stevenson and Woods, 2006 and references therein), and one that is exclusive to lizards (tailbase size). (1) Body Mass Index (BMI) is a ratio index computed as body mass (kg) divided by the square of SVL (meters). BMI is most commonly applied to humans, but has also been used for estimating condition in reptiles, particularly snakes (e.g. Madsen and Shine, 1999, 2002). (2) Fulton's condition factor (K), another ratio index computed as body mass (kg) divided by the cube of body length (kg) (weight/SVL^3) (Fulton, 1904). K assumes isometric growth because length is raised to the 3rd power. (3) Mass$^{0.3}$ SVL^{-1} index, referred to here as the Ratio index, is often used as a surrogate

predictor of condition in reptiles (e.g. Bjorndal et al., 2000; Guarino et al., 2002; Berger et al., 2005). (4) The Residual index, based on residuals from a regression of body mass on body size (Brown, 1996). This index of residuals is often used in reptiles (e.g. Shine and Madsen, 1997; Blouin-Demers et al., 2005). (5) The Relative Mass Index (RMI) is defined as log(M/M′), where M is the observed mass and M′ is mass predicted from length (L), and M/M′ is relative mass (usually expressed as a percentage). Log(M/M′) is equal to a residual from a regression of log M on log L. A value of CI = 0 indicates that observed mass = predicted mass (i.e. M/M′ = 1.0 or 100%), whereas a negative value of the CI indicates that observed mass is lower than expected mass. This condition index is mainly used in snakes and tortoises (e.g. Bonnet and Naulleau, 1995; Willemsen and Hailey, 2002; Willemsen et al., 2002). (6) Tail base diameter in lizards is considered to an indicator of fat deposited and hence condition (e.g. Bauwens, 1985). Donoghue (1998) used tail circumstances, which can be seen as a modification of tail base diameter in order to predict condition. Fat reserves are mainly stored in fat bodies in the tail and abdomen, and caudal fat reserves are particularly necessary to overwintering (Bauwens, 1985). Indeed, Avery (1970, 1974) showed that roughly half of the used fat reserves originated from the tail. To control for body size effects, we use the residuals of the regression of tailbase diameter versus log SVL in all analyses.

2.4. Statistical analyses

Data were analyzed using individual regressions with each CI as a lone predictor variable and exertion and sprint speed as dependent variables for each sex, season, and population. Thus, 48 regressions in total were performed. We did not use multiple regression because preliminary analyses showed that several of the CIs considered here are correlated with each other, and inclusion of several similarly-derived predictor variables therefore leads to unacceptable levels of collinearity (tolerances <0.1; Quinn and Keogh, 2002). Nonetheless, individual regressions are appropriate for this study because we are mostly interested in the amount of variance in performance variables explained by each CI (r^2), and hence inflation of type II error is not of primary concern. Because the relationship between CIs and locomotor performance might not be expected to be linear or monotonically increasing (for example, individuals burdened by large masses relative to their body size might be poorer performers than individuals of intermediate condition), we fit both linear models and non-linear quadratic functions to the data in all cases. We then tested whether the addition of a quadratic term explained significantly more variation than the linear model alone by comparing linear and non-linear models using partial F-tests. The variability of CI values across islands and seasons was compared using Levene's test of homogeneity of variance (Sokal and Rohlf, 1981).

Finally, we performed repeatability statistics in order to evaluate the ability to measure maximal performance capacity. Pearson correlation coefficients were calculated for the two best values of maximum sprint speed ($N = 444$) and of a subset of sample size for exertion ($N = 41$). All statistical

analyses were carried out using R 2.5.0 (http://www.cran.r-project.org).

3. Results

Although individual CIs significantly predicted exertion and/or sprint speed in several cases, no CI emerged as a consistent predictor of locomotor performance across sexes, seasons and populations (Tables 1 and 2). Indeed, with the sole exception of fall Pod Kopište females, there is even little consistency within sex/population/locomotor type. For example, whereas exertion capacity is predicted by Fulton and Residual CIs in spring males from Pod Mrčaru (Table 1), no CI predicts exertion in either fall males from Pod Mrčaru (Table 1) or spring males from Pod Kopište (Table 2). Similarly, while several CIs predict exertion and sprint speed in fall females from Pod Kopište (Table 2), those same CIs hold no predictive value in either fall females from Pod Mrčaru (Table 1) or spring females from Pod Kopište (Table 2). Of the few occasions where CIs did significantly predict performance, quadratic models explained significantly more variation in locomotor performance than linear models in three out of eight cases. Thus, relationships between CIs and performance, where they exist, may show significant curvature. Finally, comparison of variances in CIs across islands and seasons show that the six CIs tested here do not all reflect variance in male or female condition equally (Table 3). Maximum sprint speed was repeatable (Pearson correlation coefficient $= 0.92$; $P < 0.001$; $N = 444$), as was exertion (Pearson correlation coefficient $= 0.76$; $P < 0.001$; $N = 41$).

4. Discussion

If condition indices are to be of use to evolutionary ecologists and conservation biologists, they should be ecologically relevant, and hence be linked to some quantifiable measure of individual fitness and/or survival. Here, we show that six commonly used condition indices hold little predictive value for indicating two kinds of locomotor performance within two isolated island populations of the lizard *Podarcis sicula* across different sexes and seasons. Although individual CIs did predict performance in some specific ecological contexts (particularly in fall Pod Kopište females; Table 2), no one CI emerged as a consistently useful indicator of maximum laboratory performance. Indeed, whereas five out of the six CIs we tested significantly predicted a performance trait in at least one context, no indices predicted performance in more than two of the eight contexts examined. These results are consistent with a previous study showing that changes in body condition measured using a residual index do not affect sprint speed in the lizard *Iberolacerta cyreni* (Amo et al., 2007), as well as previous work examining utility of enzymatic and biochemical indices for predicting performance (e.g. Gibb and Dickson, 2002; Odell et al., 2003; but see Hammond et al., 2000). Pérez-Tris et al. (2004) also examined whether losing mass under the risk of predation may be a strategy to improve locomotor performance, but did not find any effect of body mass on locomotor performance. Thus, the morphological indices examined lack the generality that is an essential feature of a useful indicator of (locomotor) performance (a key determinant of overall fitness), and hence can only be of limited value to evolutionary ecology and conservation management. However, there is previous evidence that body

Table 1 – Regression of each condition index vs. exertion and sprint speed in Pod Mrčaru males and females for both spring and fall. Significant values are in bold

Pod Mrčaru

Index	Spring males				Spring females			
	Exertion (N = 70)		Sprint speed (N = 70)		Exertion (N = 57)		Sprint speed (N = 58)	
	r^2	P	r^2	P	r^2	P	r^2	P
BMI	0.012	0.366	0.011	0.378	0.005	0.611	0.003	0.685
Fulton	0.073	**0.021**	0.009	0.413	0.0001	0.808	0.030	0.192
Ratio	0.030	0.141	0.001	0.793	0.0002	0.898	0.0003	0.894
Residual	0.061	**0.035**	0.002	0.720	0.0002	0.917	0.016	0.348
Tailbase	0.031	0.144	0.032	0.141	0.003	0.681	0.019	0.301
RMI	0.012	0.358	0.005	0.573	0.0001	0.936	0.0001	0.984
Index	Fall males				Fall females			
	Exertion (N = 27)		Sprint speed (N = 20)		Exertion (N = 70)		Sprint speed (N = 67)	
	r^2	P	r^2	P	r^2	P	r^2	P
BMI	0.070	0.181	0.006	0.741	0.007	0.503	0.022	0.228
Fulton	0.014	0.561	0.041	0.390	0.0002	0.907	0.0001	0.913
Ratio	0.050	0.260	0.005	0.764	0.005	0.573	0.012	0.372
Residual	0.0007	0.898	0.020	0.554	0.0007	0.826	0.0009	0.807
Tailbase	0.151	0.045	0.052	0.335	0.021	0.233	0.0007	0.833
RMI	0.080	0.159	0.018	0.568	0.005	0.549	0.011	0.388

Table 2 – Regression of each condition index vs. exertion and sprint speed in Pod Kopište males and females for both spring and fall. Significant values are in bold. Note – cases where non-linear (quadratic) regression models explain significantly more variance than linear regressions are marked with an *

Pod Kopište

Index	Spring males				Spring females			
	Exertion (N = 31)		Sprint speed (N = 33)		Exertion (N = 76)		Sprint speed (N = 77)	
	r^2	P	r^2	P	r^2	P	r^2	P
BMI	0.0005	0.907	0.034	0.320	0.007	0.473	0.020	0.230
Fulton	0.073	0.156	0.0001	0.949	0.022	0.691	0.003	0.648
Ratio	0.004	0.731	0.042	0.267	0.006	0.515	0.014	0.319
Residual	0.069	0.168	0.003	0.768	0.007	0.490	0.0004	0.862
Tailbase	0.104	0.078	0.0007	0.886	0.001	0.769	0.0007	0.817
RMI	0.0002	0.941	0.051	0.223	0.006	0.505	0.009	0.415
Index	**Fall males**				**Fall females**			
	Exertion (N = 42)		Sprint speed (N = 43)		Exertion (N = 70)		Sprint speed (N = 70)	
	r^2	P	r^2	P	r^2	P	r^2	P
BMI	0.0003	0.909	0.011	0.497	0.057	**0.046**	0.0904	**0.016***
Fulton	0.025	0.317	0.010	0.512	0.025	0.195	0.008	0.456
Ratio	0.005	0.662	0.012	0.479	0.08	**0.018**	0.051	0.104*
Residual	0.018	0.394	0.004	0.673	0.0001	0.976	0.084	**0.015**
Tailbase	0.0002	0.939	0.033	0.242	0.034	0.127	0.094	**0.01***
RMI	0.002	0.761	0.009	0.535	0.083	**0.016**	0.089	**0.012**

condition may influence fitness of individuals (Blums et al., 2005), without necessarily influencing locomotor performance (Pérez-Tris et al., 2004; Amo et al., 2007). Condition might be a good predictor for over wintering survival (Blums et al., 2005) or a higher breeding probability (Anderson et al., 2001). Therefore, it is exaggerated to conclude that body condition is not a good measure of individual quality in general.

Although our data suggest little functional utility for CIs as indicators of performance, it is important to note that our study deals only with maximum laboratory performance. Previous studies have shown that lizards may not consistently use maximum locomotor performance in nature, but typically perform at levels far lower than their maximum locomotor capacities (i.e. ecological performance; see Irschick and Garland, 2001; Irschick, 2003; Irschick et al., 2005; Husak and Fox, 2006). One may therefore argue that individual condition, as estimated by morphological CIs, might instead convey information on ecological performance, as opposed to

maximum laboratory performance, which we measured here. However, we find this scenario unlikely. If morphological CIs do indeed reflect energetic status, than this should be reflected in maximum performance rather than potentially sub-maximal ecological performance. This is because while individuals who are of poor energetic or physiological status may be able to attain sub-maximal performance just as easily as physiologically "better" individuals, physiological status should set an upper limit on performance such that low-condition individuals are unable to attain maximum performance levels comparable to high-condition individuals. In other words, maximum performance is a more indicative of the health or physiological status than ecological performance. Nonetheless, data on the relationship between various morphological CIs and ecological performance are needed to resolve this issue.

An important point in favor of the use of CIs is that morphological indices have previously been shown to be useful indicators of lipid stores in some animal species (e.g. Weatherhead and Brown, 1996; Ardia, 2005), thereby conveying information on individual energetic status. However, while we did not evaluate energetic stores directly in this study, our data shows that variation in several of the morphological CIs we studied here does not follow any pattern that might be expected of an energetic index. If CIs do indeed indicate individual energetic state, then one might expect variance in CIs to change significantly across seasons both as a function of resource availability (and hence differential access to resources as a result of asymmetries in territory possession), and because some lizards may expend more energy than others during the breeding season (Marler et al., 1995; Abell, 2000; Angilletta and Sears, 2000; Schwartz et al., 2007). Differences in condition might be expected to be

Table 3 – Comparisons of morphological CI variance across seasons and islands within each sex. Significant values are in bold

CI	Males			Females		
	F	df	P	F	df	P
BMI	10.901	3,177	**<0.001**	10.060	3,289	**<0.001**
Fulton	2.863	3,177	**0.038**	7.902	3,289	**<0.001**
Ratio	1.397	3,177	0.245	1.389	3,289	0.246
Residual	3.530	3,177	**0.016**	2.731	3,289	**0.016**
Tailbase	28.884	3,177	**<0.001**	26.6	3,289	**<0.001**
RMI	0.696	3,177	0.555	1.681	3,289	0.171

particularly evident between the two populations studied because previous work has shown that Pod Kopište lizards experience higher predation pressures than those on Pod Mrčaru, and hence likely suffer higher energetic costs associated with predator avoidance (Vervust et al., 2007). Contrary to this prediction, our analyses show that CI variances change significantly across sexes, seasons and populations in only four of the six CIs considered (Table 3). The Ratio and RMI indices therefore suggest that variance in condition is constant, a result that is inconsistent with previous findings from other lizard species (e.g. Amo et al., 2006, 2007). Our results therefore cast doubt not only on the ecological relevance of CIs (at least in terms of locomotor performance) but also on the ability of these particular CIs to predict individual energetic status in this species. One further caveat is that while morphological CIs may hold little utility for predicting locomotor performance, it is nonetheless possible that CIs may correlate with other important, and possibly sex-specific, fitness components such as female reproductive output. Future studies might consider examining links between CIs and a range of traits impacting fitness in various animal species.

5. Conclusion

Our data suggests that condition indices based on simple morphological measurements are not generally useful indicators of locomotor performance traits in P. sicula. Furthermore, it is currently unclear whether all of these CIs do in fact indicate overall energetic status in this species. Alternatives to morphological CIs such as measurements of blood condition, and various hormonal, immunological, or enzymatic assays (reviewed in Stevenson and Woods, 2006) have thus far yielded similarly inconsistent results with regard to locomotor performance where they have been tested (e.g. Gibb and Dickson, 2002; Odell et al., 2003). Nonetheless, the physiological and ecological validation of such indices is necessary, particularly if condition proxies are to be used in conservation management. We therefore encourage researchers to examine the predictive value of all commonly used condition indices for important ecological and physiological variables (e.g. Ardia, 2005). Experimental studies examining the effects of manipulating individual condition would be especially valuable.

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