

Fluctuating Asymmetry, Physiological Performance, and Stress in Island Populations of the Italian Wall Lizard (*Podarcis sicula*)

BARI VERVUSTI,^{1,2} STEFAN VAN DONGEN,¹ IRENA GRBAC,³ AND RAOUL VAN DAMME¹

¹Department of Biology, University of Antwerp, B-2610 Wilrijk, Belgium

³Department of Zoology, Croatian Natural History Museum, Demetrova 1, HR-10000 Zagreb, Croatia

ABSTRACT.—The use of fluctuating asymmetry (FA) as a measure of developmental instability, and its relationship to stress and fitness, is highly controversial. Here, we present results from a preliminary study comparing levels of asymmetry in various characteristics between two island populations of the Italian Wall Lizard (*Podarcis sicula*), one of which was recently founded. We relate individual asymmetry to several measures of physiological performance. Levels of FA varied clearly among the traits studied. Repeatability of FA estimates was high for meristic traits but low for metric traits. Levels of FA were on average higher in the newly founded population. We found a significant decrease in exertion (time until exhaustion by continuously chasing) with increasing levels of fluctuating asymmetry (i.e., more symmetric individuals had a higher exertion). Speed of locomotion showed a positive trend with increasing FA. No relationship was found between individual levels of FA and bite force. These results suggest that FA estimates, based on the accurate measurement of several traits, may be useful in explaining differences in developmental stability and physiological performance at the individual and population level.

The use of fluctuating asymmetry (FA, small random deviations in the development of both sides of a bilateral symmetric character) as an indicator of stress or fitness (Van Valen, 1962) has long been a contentious issue in conservation biology and evolutionary biology. The idea that FA reflects developmental instability (DI, the inability to buffer development against random noise; Klingenberg, 2003) and, therefore, should correlate positively to stress and negatively to fitness, is appealing but has drawn much criticism regarding FA's use and relevance (e.g., Lens et al., 2001; Polak, 2003; Van Dongen, 2006). Population levels of FA have been proposed as useful early warning indicators for conservation biology, but although several studies have found a positive relationship between FA and environmental stress (e.g., Valentine et al., 1972; Pankakoski et al., 1992; Clarke, 1993; Hardersen, 2000), others have not (e.g., Rabitsch, 1997; Polak et al., 2002). Likewise, at the level of individual selection, the idea that large values of FA should reflect lower quality in terms of fitness (reviewed in Leung and Forbes, 1997; Møller, 1997, 1999) has received mixed support (Clarke, 1995, 1998). The ambiguous nature of these results has likely contributed to the recent decrease in popularity of FA (Van Dongen, 2006). We argue that the causes of these disparate findings are themselves of interest, and should be understood

before a potentially useful tool is cast aside prematurely. Of particular importance is the need to understand how various forms of stress affect DI and FA and how this relates to individual fitness and performance. This research should ideally be carried out on a variety of species and populations, using different kinds of paired traits, on large sample sizes, and using a correct statistical protocol (Van Dongen, 2006).

There are surprisingly few asymmetry studies of lizards. This is unexpected, given that these animals possess many paired characteristics that can be measured (e.g., limbs, eyes, head dimensions) or counted (e.g., multiple types of scales, femoral pores) with relative ease (Soulé, 1967). In addition, lizards have proved excellent model organisms in behavioral, ecological, and eco-morphological studies. At the population level, high levels of FA are associated with genetic stress (inbreeding) and small island size in *Uta stansburiana* (Soulé, 1967; Soulé and Yang, 1973; Soulé et al., 1974) and in *Trachydosaurus rugosus* (Sarre and Dearn, 1991). Likewise, *Oedura reticulata* and *Gehyra variegata* in small habitat fragments exhibit high levels of FA (Sarre, 1996). In contrast, the small island populations of the lacertid *Podarcis muralis* in Lake Skadar (Montenegro) do not show an increase in FA (Cinobrinja-Isailovic et al., 2005). At the individual level, incubating lizard eggs at suboptimal temperatures results in more asymmetric juveniles in *Calotes versicolor* (Ji et al., 2002) and *Sceloporus virgatus* (Qualls and Andrews, 1999), suggesting that environmental

²Corresponding Author. E-mail: bart.vervusti@ua.ac.be

stress may be an important cause of FA in lizards. In a hybridization experiment with two species of the *Sceloporus grammicus* complex, Dosselman et al. (1998) found no evidence for increased FA in hybrid against parental individuals.

Evidence that FA may correlate with survival or reproductive success in lizards is mixed. In the lacertids *Iberolacerta monticola* (López and Martín, 2002) and *Psammodytes algirus* (Martín and López, 2001), males with more asymmetrical femur lengths have lower escape speeds. In contrast, no relationship exists between hind-limb asymmetry and running speed in hatchling *Amphibolurus muricatus* (Warner and Shine, 2006). Intriguingly, *I. monticola* females prefer the scent of more symmetric males (Martín and López, 2000; Martín et al., 2006), implying a potential role for FA in mate selection in this species. Likewise, there is evidence for a possible role of FA as a determinant of mating success in *I. monticola* (Martín and López, 2006) but not in *Anolis carolinensis* (Lailvaux and Irschick, 2006).

Here, we describe the results of a study on FA patterns in two island populations of the lizard Italian Wall Lizard, *Podarcis sicula*. Lizards on one of these islands are the descendants of a founder population consisting of five males and five females, introduced in 1971 and, therefore, present a unique opportunity to examine the consequences of this recent bottleneck on FA. We compare levels of FA between the two populations and relate individual asymmetry to performance measures.

MATERIALS AND METHODS

Species and Study Site.—During April and September 2006, we captured (by noose) 313 *P. sicula* on two neighboring islets in the Adriatic Sea: Pod Mrčaru (42°46'N, 16°46'E; area = 0.03 km²; N = 167) and Pod Kopište (42°45'N, 16°43'E; area = 0.09 km²; N = 146). The islets resemble each other closely in most aspects of their physiognomy. Both consist of organic limestone and have a central, vegetated zone (rising up to 20 m on Pod Mrčaru and to 30 m on Pod Kopište), encircled by an almost barren rocky belt. Plant cover on Pod Mrčaru consists mainly of annuals: *Lavatera arborea*, *Lotus edulis*, *Portulaca oleracea*, *Allium ampeloprasum*, and *Cynodon dactylon* in the center, and *Crithmum maritimum* in the periphery. Pod Kopište has some low bushes of *Pistacia lentiscus* and *Juniperus excelsa*; the central part is covered mainly by *Chenopodium murale*, *Cynodon dactylon*, and *Asparagus officinalis*; *Crithmum maritimum* is the dominant species on the rocky fringes (Vervust et al., 2007). The population on

Pod Mrčaru consists of the descendants of a propagule of 10 individuals (five males, five females) taken from Pod Kopište and released on the island in 1971 (Nevo et al., 1972).

The Italian Wall Lizard, *P. sicula*, is a robust, ground-dwelling, diurnal, heliothermic, actively foraging lacertid lizard (adult snout-vent [SVL] length 55–70 mm), which occupies a variety of semiopen habitats in the Mediterranean (Henle and Klaver, 1989). Adult males have larger heads, longer hind limbs, and better developed femoral pores than do females. In the analyses, we considered two age classes: juveniles (born in the current activity season) and adults (born earlier). These age classes can be recognized readily on the basis of SVL. Henle and Klaver (1989) provide detailed information on the general biology of *P. sicula*.

Measurement of Morphological Characteristics.—Lizards were individually stored in cloth bags and transported to the field station on the nearby island of Lastovo. Lizards were measured to the nearest 0.01 mm using electronic callipers (CD-20PP, Mitutoyo Corporation, Japan). We measured head height, head width, head length, lower jaw length, length of the quadratum, and length of the coronoid. Head height was defined as the greatest distance from the highest portion of the head to the bottom of the lower jaw; head length as the distance between the tip of the snout and the posterior side of the parietal scales; and head width as the greatest distance between the external sides of the parietal scales. The lower jaw length was measured between the anterior tip of the dentale and posterior articulare; the quadratum from the fenestra temporale to the posterior end of the os quadratum; and the coronoid between the anterior tip of the fenestra temporale and tip of the snout. The length of the lower jaw, quadratum, and coronoid were measured twice on each side.

To quantify the variation in scale numbers, we took pictures of both sides of the head using a digital reflex camera Nikon D70 with 105 mm micro-nikkor lens (Nikon, Japan). On these pictures, we counted the following head scales: the supraciliaria, ocularia, supralabialia, sublabialia and the sum of temporalia and auricularia (Fig. 1). The supraciliaria consist of a row of scales above the eye. The ocularia border the eye ventrally. The supralabialia are the scales bordering the mouth, from the rostrale to the corner of the mouth. The sublabialia line the lower jaw from the mentale to the corner of the mouth. The temporalia and auricularia are dorsally bordered by the parietalia and ventrally by the supralabialia. We also took pictures of the inner legs to quantify the number of femoral pores. These pores are the openings of follicular



FIG. 1. Head used in this study. Mentale; SpC = supralabialia; aur = auricularia.

glands in the corner of the mouth along the ventral side of the head. To explore the relationship between FA and performance, we measured all individuals (N = 313).

Performance.—We measured maximal sprint speed and bite force for each individual. For sprint speed, we used a 10 m race track on a large outdoor thermoregulated arena (Bennu et al., 1990), using an electronic timing system (0.1°C).

Maximal sprint speed was measured by chasing lizards on a 10 m racetrack with a consistent effect (repeated measures ANOVA) that lizards did not change their sprint speed over any photoperiod. We considered an individual's sprint performance to be judged to be run continuously. Berkum and P (not included in the analysis).

Exertion was measured by chasing lizards (1 m diameter hausted) when they were exhausted after 10 consecutive sprints (in seconds) at the end of the exertion (Bennu

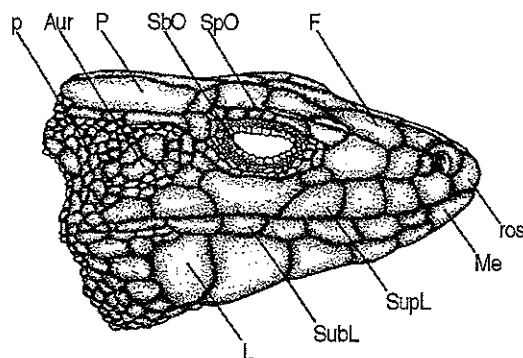


FIG. 1 Head of *Podarcis sicula* showing the scales used in this study. Abbreviations: ros = rostrale; men = mentale; SpO = supraciliaria; SbO = ocularia; SpL = supralabialia; SbL = sublabialia; Temp = temporalia; aur = auricularia; P = parietale

glands in the dermis and occur as a single series along the ventral side of the thighs (Cole, 1966). To explore the degree of measurement error, we recounted all meristic traits on a subset of 31 individuals (Palmer, 1999).

Performance Measurements.—We estimated maximal capacity for running speed, exertion, and bite force in each individual lizard. Prior to each performance trial, lizards were allowed to rest for at least one hour (maximally, 1.5 h) in large outdoor terraria in which they could thermoregulate freely. At the start of each measurement, we made sure that the lizard's cloacal body temperature was within the optimal range for sprinting (34–37°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. We found no consistent effect of trial on maximal sprint speed (repeated measures ANOVA, $P > 0.3$), indicating that lizards did not fatigue over trials. 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. Some trials (< 5%) were judged to be bad because lizards did not run continuously. Such "bad" trials (e.g., van Berkum and Tsuji, 1987; Tsuji et al., 1989) were not included in the analyses that follow.

Exertion was estimated by continuously chasing lizards along a horizontal torus track (1 m diameter). We considered lizards "exhausted" when they no longer responded to 10 consecutive (gentle) taps on the dorsum. The time (in seconds) elapsed between the start and the end of the run was taken as a measure of exertion (Bennett, 1980). Because this procedure

is demanding (for the lizard and the experimenter), each individual was tested only once. However, earlier measurements on a smaller sample of specimens showed that the procedure yields very repeatable results (BV, pers. obs.).

Bite forces were measured using an isometric Kistler force transducer (type 9203, Kistler, Inc., Winterthur, Switzerland) mounted on a purpose-built holder and connected to a Kistler charge amplifier (type 5058 A, Kistler, Inc.). All the animals were induced to bite on two plates, fixed at a distance of 3.65 mm. Bite forces were recorded using a portable computer equipped with an A/D converter (PC-Scope 1512, Imtec GmbH, Backnang, Germany). For a full description of the measuring device, see Herrel et al. (2001a,b). In each animal, bite-force was measured five times. We considered the maximum value as the maximum bite force for that individual lizard.

Upon completion of the measurements, the lizards were marked (individual toe-clip codes) and released at the exact site of capture. This was always within two days.

Statistical Analysis.—Three issues that need to be addressed when estimating asymmetry are measurement error (ME), the occurrence of other forms of asymmetry, and the degree of association between individual levels of asymmetry and the underlying process of developmental instability (Van Dongen, 2006). Therefore, we conducted a first set of analyses to establish degrees of ME and to explore potential directional asymmetry, following guidelines detailed by Van Dongen (2006). Next, we examined differences in the degrees of asymmetry between the two islands and assessed associations with performance measures, using a linear mixed model with repeated-measures structure. The different trait-specific asymmetry values were used as dependent variables, whereas island, sex, age, and the three performance measures were added as independent variables. Because the different asymmetry values for each individual are statistically dependent, we adopted a repeated-measures analysis procedure by treating "individual" as a random effect. Asymmetry values were \log_{10} -transformed and standardized (Z-transformation) for each trait. We also analyzed for possible correlations between either DA or FA. The three performance measures were analyzed after \log_{10} -transformation. All analyses were performed in SAS (version 9.1, SAS Institute, Cary, NC).

RESULTS

Measurement Error and Directional Asymmetry.—The amount of ME differed strongly

TABLE 1. Average degree of asymmetry (unsigned fluctuating asymmetry, FA) with standard deviation (SD), average numbers on left and right side (R/L), *t*-test for directional asymmetry (DA; **: $P < 0.01$, all others $P > 0.05$), and degree of measurement error (ME, as percentage of the average degree of asymmetry) in the meristic traits on the basis of 31 individuals for which these traits were counted twice.

Trait	Unsigned FA (SD)	R/L and test for DA	Degree of ME (%)
Femoralia	1.37 (1.03)	20.6/20.3, $t_{30} = 0.78$	0
Temporalia	1.98 (1.45)	72.5/72.3, $t_{30} = -0.25$	5
Supraciliaria	0.65 (0.75)	6.6/6.1, $t_{30} = 3.38^{**}$	0
Ocularia	5.55 (6.45)	18.0/18.0, $t_{30} = 0.19$	4
Supralabialia	1.15 (1.03)	7.5/8.0, $t_{30} = -1.76$	0
Sublabialia	0.48 (0.57)	6.6/6.7, $t_{30} = -0.24$	0

between meristic and metric traits. In comparison to the degree of asymmetry, ME was extremely low in the meristic traits but high in the metric characters (Tables 1–2). The repeatabilities of FA in the metric traits were so low that we decided to eliminate them from all further analyses.

We found evidence for directional asymmetry in one meristic trait, the number of supraciliaria (Table 1). One individual had one ocular scale more on the left side than on the right, and 14 individuals had more supraciliaria on the right side. In 10 of these 14 cases, there was a difference of one scale; in the remaining four cases there was a difference of two scales. The remaining 16 individuals were symmetric. We chose not to correct for this case of directional asymmetry, because this would result in the awkward situation that the perfectly symmetrical individuals would become asymmetrical in the analyses. For the metric traits, no directional asymmetry was detected (Table 2). Correlations in asymmetry among traits were weak and not statistically significant.

Variation in Asymmetry and Relation to Performance—The mixed-model analysis indicates that, on average, the degree of FA differs between islands; however, the difference was

TABLE 2. Summary of mixed regression analysis separating real fluctuating asymmetry (FA) from measurement error and testing for directional asymmetry in the three metric traits. The fixed side effect tests (*F*-test) for directional asymmetry, and the ratio of the variation caused by real FA over the degree of measurement error, reflect the repeatability of the measurement of FA.

Trait	Test for DA	Repeatability of FA
Lower jaw	$F_{1,41} = 0.25, P = 0.62$	0% ^a
Quadrate	$F_{1,41} = 0.28, P = 0.60$	0% ^a
Coronoid	$F_{1,41} = 2.20, P = 0.15$	29% ^a

^aNone of the variations resulting from real FA were statistically significant as tested by the likelihood-ratio test (all $P > 0.2$).

not the same for each trait (Table 3, significant island \times trait interaction). It also reveals an association between exertion and the level of FA, a relationship that is unaffected by any FA trait (no significant trait \times exertion interaction, Table 3). A graphical comparison of the different performance measures between the 50% most asymmetrical and symmetrical individuals shows that symmetric individuals have a higher exertion capacity (Fig. 2). The graph also suggests a tendency for asymmetrical individuals to have higher speeds (Fig. 2), but this was not supported by the statistical analysis (Table 3).

Differences in average FA between the two populations were statistically significant for the supraciliaria (estimated difference \pm SD = 1.02 ± 0.19), supralabialia (0.70 ± 0.17), sublabialia (0.71 ± 0.18), femoralia (0.45 ± 0.18), and ocularia (0.40 ± 0.18); in each case, the recently founded population was the more asymmetrical. For the temporalia + auricularia, the difference (0.19 ± 0.19) was in the same direction but did not reach statistical significance. A description of the meristic traits for each insular population is given in Table 4.

DISCUSSION

Our study system clearly suffers from the problems associated with inferring effects from two-population comparisons (Garland and Adolph, 1994). Still, some explanations seem more likely than others. Population-level differences in FA have been ascribed to two types of developmental stress: environmental perturbations; and stress resulting from changes in the genetic organization of individuals and populations (Clarke, 1995). Increased FA is associated with the presence of pollutants, such as PCBs, heavy metals, radioactive radiation, UV radiation, and excess artificial fertilizer, in a wide range of organisms (e.g., Eeva et al., 2000; Møller, 2000; Marques et al., 2005; Voets et al., 2006; but for counterexamples, see Clarke, 1998; Björkstén et al., 2001; Woods et al., 2002).

TABLE 3. O mixed model between the two islands with the three

Source
Island
Age
Sex
Speed
Exertion
Bite force
Island \times trait
Age \times trait
Sex \times trait
Speed \times trait
Exertion \times trait
Bite force \times trait

However, did the two populations be the result of two islands likely a very similar and their egg abiotic conditions responsible for the two populations. Mrčaru is cohabited by Pod Kopište island inter aggressively.

FIG. 2. Meristic traits of most symmetrical (PM) and most asymmetrical (Me) individuals are shown.

TABLE 3. Overview of significance tests in the mixed model comparing levels of asymmetry between the two islands and testing for associations with the three performance measures.

Source	F-statistic	df 1	df 2	P-value
Island	47.9	1	129	<0.001
Age	0.08	1	120	0.78
Sex	0.00	1	126	0.96
Speed	1.98	1	119	0.1
Exertion	5.69	1	126	0.02
Bite force	0.01	1	122	0.94
Island × trait	2.63	5	560	0.02
Age × trait	0.49	5	526	0.79
Sex × trait	0.30	5	525	0.91
Speed × trait	0.19	5	521	0.97
Exertion × trait	0.83	5	524	0.53
Bite force × trait	60.5	526	0.70	

However, differences in FA observed between the two populations of *P. sicula* here are unlikely to be the result of environmental differences; the two islands lie very close to each other and have a very similar physiognomy; therefore, lizards and their eggs are likely exposed to nearly equal abiotic conditions. Therefore, differences in the biotic environment are a more likely to be responsible for the differences in FA between the two populations. The population on Pod Mrčaru is considerably denser than the one on Pod Kopsište, and the lizards on the former island interact far more frequently and more aggressively (Vervust et al., unpubl). Compet-

itive stress is associated with increased FA in several organisms (e.g., Rettig et al., 1997; Pelabon and Van Breukelen, 1998; Sullivan, 1998). Parasites are yet a further cause of stress that can induce FA (Møller, 2006), but we have no indication that the level of parasitism differs between the two populations of *P. sicula* under study.

Although population density and competitive stress may affect FA at a proximate level, a more likely ultimate cause for the increased level of FA on Pod Mrčaru is the genetic history of this population. The population was founded in 1971 (about 17 generations ago) with the experimental introduction of 10 adult lizards from Pod Kopsište (see Nevo et al., 1972). Although we have currently no genetic information on the Pod Mrčaru lizards, it seems reasonable to assume that such a severe bottleneck should have had an impact on the genetic diversity of the population (Wright, 1931, 1978; Gilpin, 1991; Lande, 1995; Lynch et al., 1995). Moreover, the source population on Pod Kopsište is likely itself to be the product of a founding event in historical times, and most probably *P. sicula* underwent a series of bottlenecks, "hopping" from one island to another, before arriving on Pod Mrčaru (Kammerer, 1926). Such serial bottlenecking may promote genetic erosion (i.e., loss of genetic diversity over time; Hewitt, 2000). Fluctuating asymmetry has been associated with inbreeding and loss of heterozygosity (e.g., Clarke et al., 1986, 1992;

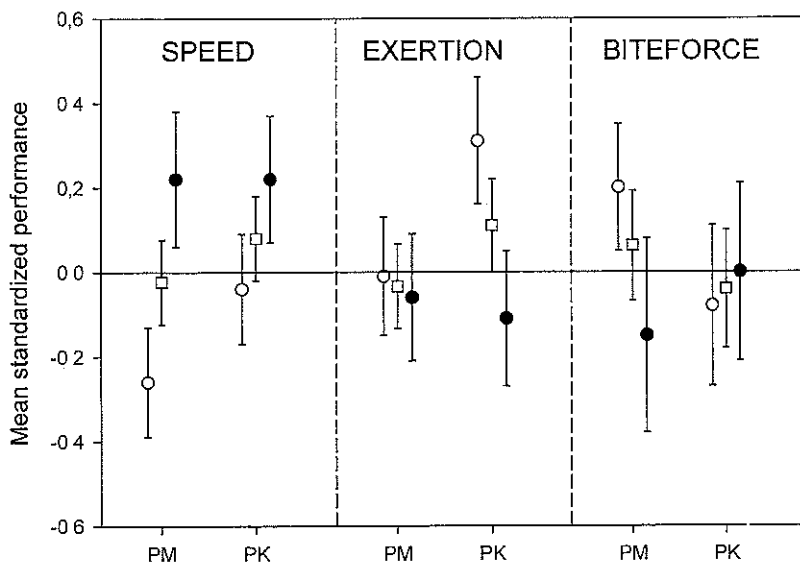


FIG. 2. Mean (\pm SD) standardized speed, exertion and bite force for lizards from two populations (PK: Pod Kopsište; PM: Pod Mrčaru). Overall means for the entire population (open squares) and the means for the 50% most symmetrical specimens (closed circles) and the 50% most asymmetrical individuals (open circles) are shown.

TABLE 4. Overview of phenotypic traits for adult male and female *Podarcis sicula* from Pod Mrčaru and Pod Kopašte. Abbreviations: M = median; SD = standard deviation; and R = range, on both right and left sides.

	Ocularia		Supraciliaria		Supralabialia		Sublabialia		Temporalia + auricularia		Femoral pores				
	M	SD	R	M	SD	R	M	SD	R	M	SD	R			
Right															
Males															
Pod Mrčaru	19	2.12	12	6	1	5	6	0.066	4	79	13.65	66	21	1.78	10
Pod Kopašte	20	2.56	8	7	0.568	8	2	/	0	77	6.95	18	22	1.43	4
Females															
Pod Mrčaru	19	1.92	8	8	0.861	3	6	0.46	1	72	10.42	38	21	1.63	7
Pod Kopašte	19	1.92	9	7	0.416	2	4	/	0	71	12.52	48	21	1.33	6
Left															
Males															
Pod Mrčaru	18	2.31	10	8	0.913	4	7	0.618	3	74	11.87	64	22	1.87	9
Pod Kopašte	20	1.17	3	8	0.422	1	1	0.422	1	71	5.33	14	22	0.99	3
Females															
Pod Mrčaru	18	2.24	9	8	1	5	5	0.663	4	72	11.31	56	21	2.07	7
Pod Kopašte	19	1.49	7	7	0.577	4	3	/	0	74	9.86	43	20	1.52	5

but see Fowler and Whitlock, 1994), phenomena typically accompanying founding events. Several studies have found higher levels of FA in populations that went through a recent bottleneck (e.g., Wayne, 1986; Hoelzel et al., 2002), but the generality of this result is debated (for contrary findings, see Kieser and Groeneveld, 1991; Brookes et al., 1997; Suchentrunk et al., 1998). Why bottlenecks produce higher levels of FA in some and not in other species remains an open question.

Outbreeding may present another source of genetic stress, and this stress may result in increased FA (review in Clarke, 1995). The only study that has tackled the issue in lizards (Dosselman et al., 1998) did not find support for this idea.

The value of FA for evolutionary biology and conservation practice critically depends on its relationships with fitness. Early evidence that FA correlated negatively with growth, fecundity, and longevity (review in Møller, 1997) fed the hope that FA could be used as a convenient proxy for fitness. More recently, however, it has become apparent that the relationships between FA, DL, and fitness are far from clear (Polak, 2003), and the appeal of the index seems to be fading somewhat (Van Dongen, 2006). Examining the relationship between FA and fitness components, using different traits, in different populations and under different circumstances, may help in evaluating the usefulness of the index as an experimental and monitoring tool (Van Dongen, 2006). Our results indicate a negative relationship between FA and maximal exertion capacity; more symmetric lizards ran for longer periods when chased continuously. The capacity for prolonged locomotor activity is considered of direct ecological relevance in lizards (Garland, 1999; Sinerchia et al., 2000), especially under harsh conditions such as low food availability (LeGalliard et al., 2004). Because it depends on the performance of a variety of morphological, biochemical, and physiological characteristics (Garland, 1984), it may also constitute a biomarker of the general "vigor" of an animal. In this respect, it is encouraging to find that FA and exertion covary in parallel for different traits and in both populations. In contrast to earlier studies on lacertids, we found no relationship between FA and maximal sprint capacity. However, it should be noted that the other studies (Martín and López, 2001) measured FA on characteristics implicated in locomotion (limb dimensions); thus, such a relationship may be expected on a direct functional basis. The large measurement error on our metric characteristics precluded a reliable test (Palmer, 1999). The great difference in repeatability between metric and meristic

traits can partly be explained by the fact that they were used and photographs.

We would like to address some general methodological issues. First, because the mean FA is sensitive to the degree of reliable substrate (Palmer, 1999), the traits exhibit similar results and similar retest performance, highlighting some general methodological issues. First, the effect of FA on the retest performance proved difficult because these results are more accurate than those from and crural length studies (see above). Measurements may be affected by technical problems.

To understand the use of FA as an indicator (aspects of) fitness, in different degrees of kinship, a study will encompass subjects in the conservation area in addition to their organisms in morphology, as they seem "exapted" to possess an exceptional meristic traits (also Seligmann 2006).

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traits can partly be caused because live animals were used and counts were done on the same photographs

We would like to end with some methodological issues. First, our results indicate that, because the measurement error is small relative to the degree of FA, scale counts constitute a reliable substrate for studying FA in lizards (Palmer, 1999). Also, FA for the different scale traits exhibits similar between-island variation and similar relationships with physiological performance, hinting that they may be revealing some general capacity for buffering developmental noise. However, reliable measurement of FA on the metric variables considered here proved difficult. This was somewhat surprising, because these distances are measured more accurately than variables such as femur length and crus length, which have been used in earlier studies (see above). RX (X-ray pictures)-measurements may provide a way out of this technical problem.

To understand when and where FA can be used as an index of DI and ultimately of (aspects of) fitness, we need data on multiple traits, in different populations under different degrees or kinds of stress. We hope that our study will encourage the use of lizards as study subjects in the exploration of FA as a tool in conservation and evolutionary biology. In addition to their demonstrated value as model organisms in behavioral ecology, ecological morphology, and evolutionary biology, lizards seem "exapted" for FA studies because they possess an exceptionally rich array of paired meristic traits that can be measured reliably (see also Seligmann, 2006; Seligmann and Krishnan, 2006).

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