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Sexual size and shape dimorphism in Near Eastern fire salamander, *Salamandra infraimmaculata* (Caudata: Salamandridae)

Abdullah Altunışık*

Recep Tayyip Erdoğan University, Faculty of Arts and Sciences, Biology Department, Rize, Turkey

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Abstract
Sexual dimorphism, phenotypic difference between males and females of the same species, has been demonstrated in many invertebrates and vertebrates. In these studies, which were especially conducted on amphibians, female individuals were reported to be larger than males. However, this does not necessarily mean that this also applies to body shapes. Therefore, in this study, a total of 31 characters of body size and body shape were measured and analyzed in the Near Eastern fire salamander, in order to understand whether these characters differ between female and male individuals. The results suggest that there is a significant difference between the sexes in terms of both body size and some body shapes (e.g. arm and leg length, arm diameter, cloacal proportions) in this fire salamander. I conclude that both sexual size and shape dimorphism need to be taken into account to help understand an organism's life-history traits, ecology, population dynamics and behavior.

Keywords
Body size; morphometry; salamander; Salamandridae; sexual dimorphism; shape dimorphism

Introduction

Sexual dimorphism can be defined as shape, size and morphological differences between males and females of a species. Among them, sexual size dimorphism (SSD) is the most common phenomenon within the animal kingdom and has been the subject of many studies (Fairbarn, 1997; Monnet & Cherry 2002; Cox et al., 2003; Linderfors et al., 2007; Stillwell et al., 2010; Liao et al., 2013a; Liao et al., 2015). Although there is more emphasis on body size dimorphism in the literature,

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*) E-mail: abdullah.altunisik@erdogan.edu.tr

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there are also several studies on shape dimorphism (Ivanoviç et al., 2008; Romano et al., 2009; Labus et al., 2013; Rastegar-Pouyani & Fattahi, 2015).

It is well documented that the basic factors that elicit sexual dimorphism are generally natural selection, sexual selection and fecundity selection (Anderson, 1994; Fairbarn, 1997; Liao et al., 2013b; Liao et al., 2015). Firstly, natural selection can be hypothesed to benefit survival, for example via competition for food among individuals, and drive evolution of SSD in different directions (Fairbarn, 1997). However, this model does favor neither male nor female. Secondly, sexual selection, which is one of the most commonly used hypothesis to explain the evolution of SSD, most often favors one sex. For instance, individuals might choose their mate based on size which seems usually to result in male individuals having larger body size and a male-biased SSD. According to this hypothesis, male individuals with enlarged body size have an advantage because they can obtain higher reproductive success (Andersson, 1994). Thirdly, the direction of SSD can evolve towards larger female individuals, which can use their resources more directly than males to enhance their reproductive output (e.g. clutch size and egg size; Anderson, 1994; Liao et al., 2013b; Liao et al., 2015). As a consequence of this tendency, fecundity selection favors female-biased SSD. In addition, sexual differences in life history traits may also cause the emergence of SSD, which is a well-known population property (Cadeddu et al., 2012). Conversely, the reasons for evolving shape dimorphism might have ecological (e.g. niche sharing) or behavioral (e.g. mate choice) reasons or may be related to reproduction (e.g. anatomical and physiological differences between males and females; e.g. Rastegar-Pouyani & Fattahi, 2015).

The magnitude and extent of SSD can vary considerably across taxa (Liao et al., 2015). For instance, in lizards and mammals (Cox et al., 2003; Linderfors et al., 2007; Stillwell et al., 2010) male-biased dimorphism is prevalent; on the contrary in amphibians and insects (Fairbarn, 1997; Monnet & Cherrry, 2002; Liao et al., 2013) female-biased dimorphism is more common. More specifically, about 90% of the anurans and 61% of the urodeles indicate a female-biased sexual size dimorphism (Kupfer, 2007; reviewed in Reinhard et al., 2015).

Among the Salamandridae, a family of the Urodela order, sexual dimorphism is prevalent too. In most situations, the dimorphisms are characteristic (coloration, presence of male secondary sexual characteristics, differences in head size, tail length, etc.) but may also be more cryptic (e.g. glandular structure, pheromone secretion and epidermal texture) and must be tested statistically following morphometric measurements. Sexual dimorphism of the overall body and head measurements of salamandrids has been investigated in only a few studies (Kalezic et al., 2000; Labus et al., 2013; Reinhard et al., 2015; Xiong et al., 2016).

Here we focus on the Near Eastern fire salamander, *Salamandra infraimmaculata*, which is one of the six known representatives of the *Salamandra* genus, a member of the family Salamandridea (Amphibia: Caudata). *S. infraimmaculata* inhabits southeastern and eastern parts of Asia Minor, Turkey, Northern Iraq, Northwestern Iran, Lebanon and Northern Israel (Papenfuss et al., 2009). Although the

Near Eastern fire salamander is a rare and protected species in Northern Israel, its status is near threatened (NT) in the rest of the world (Blank & Blaustein, 2012).

So far, investigations have been confined to sexual dimorphism of other species of *Salamandra* genus, and sexual dimorphism of *S. infraimmaculata* has not been examined comprehensively. Therefore, I analyzed the sexual size and shape dimorphism of this fire salamander based on the Mezitli (mid-south part of Turkey) population. The purpose of this study was to (1) assess sexual dimorphism in Near Eastern fire salamander and to interpret the results by taking the widespread theories into consideration; and (2) to expand our knowledge regarding *S. infraimmaculata*.

Material and methods

The study site (720 m a.s.l.) is located in Mezitli, Mersin (36° 52′ N, 34° 25′ E) in the mid-south part of Turkey and has a climate that is Mediterranean and moderately continental (Altunışık, unpublished data). According to climatic data obtained from the meteorological station situated near the study site for the years 1950-2015, the average temperature during summer was 27.16°C, while it was 10.9°C in the winter (URL-1). *S. infraimmaculata* is a terrestrial and viviparous species, and individuals from the studied population were seen near a permanent pond formed by a stream.

A total of 30 adult salamanders (14 males and 16 females) were all caught by hand in the nighttime in a forested area during the breeding season in 2016 and all experiments were performed in accordance with the Turkish law and with permission for animal experiments of the local ethics committee of Recep Tayyip Erdoğan University (approval reference number: 2015/71). After sampling, all salamanders were released back to their habitats. The sexes of the individuals were determined by externally visible sexual characters (e.g., the male has a prominent cloaca).

I measured 31 variables (table 1) to the nearest 0.01 mm using a digital caliper. The sexual size dimorphism (SSD) was computed according to a formula introduced by Ranta et al. (1994): Sexual Dimorphism Index (SDI) = (size of the larger sex/size of the smaller sex)-1.

The statistical analyses were conducted by using SPSS 17 (IBM, Statistics for Windows). Since the data for all 31 variables were normally distributed (Kolmogorov-Smirnov test, $P > 0.05$) and variances were homogeneous (Levene's test), a principal component analysis (PCA) was conducted to examine size and shape dimorphism between males and females. The first principal component (PC), derived from a set of morphometric measurements, is mostly regarded as an axis of overall body size variation when all traits load largely and in the same direction (Reyment et al., 1984; Bookstein, 1985), with the remaining variance describing relative shape differences expressed in consecutive PCs (Schäuble, 2004, Zhang et al., 2014; Xiong et al., 2016). In the next step, in order to designate which characters differed between the sexes, a univariate analyses of covariance (ANCOVA) was performed, with sex as a factor and PC1 score as a covariate (Guillaumet et

Table 1.
Morphometric body and head characters.

Character	Definition
Body measures	
SVL	Snout–vent length from the tip of the snout to the posterior margin of the cloaca
OAL	Overall length
TL	Tail length from the posterior margin of the cloaca to the tip of the tail
TH	Tail height
UAL	Upper arm length from the posterior margin of the front leg (axilla) to the angle of the elbow
LAL	Lower arm length from the angle of the elbow to the wrist
LAL2	Lower arm length measured until the tip of the longest finger
TAL	Total arm length from the axilla to the tip of the longest finger
ULL	Upper leg length from the anterior margin of the hind leg (groin) to the angle of the knee
LLL	Lower leg length from the angle of the knee to the ankle
LLL2	Lower leg length measured until the tip of the longest toe
TLL	Total leg length from the groin to the tip of the longest toe
CL	Cloacal length
CW	Cloacal width
CHW	Chest width from axilla to axilla
BWM	Body width at mid-body
PW	Pelvic width
GG	Distance from groin to groin
DEX	Distance of extremities from axilla to groin
UAD	Upper arm diameter
LAD	Lower arm diameter
ULD	Upper leg diameter
LLD	Lower leg diameter
Head measures	
HL	Head length
HW	Head width at the angle of the jaw
ED	Diameter of the eye
ON	Orbit–naris distance from the anterior edge of the eye to the nostril
IO	Interorbital distance from eye to eye (measured from the centre of the eye)
IN	Internarial distance from nostril to nostril
ES	Eye–snout distance from the anterior edge of the eye to the tip of the snout
IC	Intercanthal distance from the anterior edge of the eye to the other

al., 2005; Romano et al., 2009), for each morphological variable independently. In addition, the probable difference between males and females for the independent characters was then tested by multivariate analysis of variance (MANOVA) with sex as a factor.

Results

According to results of the PCA, three principal components were extracted and they jointly explain 73.16% of the overall variation (table 2). Since the largest proportion of total variation (51.97%) was explained by the first principal component (PC1) and all independent variables loaded heavily in the same direction (positively) onto this component, the individual scores on PC1 were used to determine the variation in overall body size. The other two components (PC2 and PC3), which accounted for another 14.69% and 6.50% of the total variation, respectively, were positively or negatively correlated with the independent variables (table 2). The mean values and ranges for the morphological measurements for *S. infraimmaculata* are presented in the Appendix (table A1).

According to the ANCOVA results, eleven morphological variables (table 2) were revealed as showing significant differences in the body shape, with males having larger values than females for all these variables: upper arm length (UAL; $F_{1,27} = 10.321$, $P < 0.01$), lower arm length (LAL; $F_{1,27} = 17.838$, $P < 0.001$), lower arm length2 (LAL2; $F_{1,27} = 5.185$, $P < 0.05$), total arm length (TAL; $F_{1,27} = 11.864$, $P < 0.01$), upper leg length (ULL; $F_{1,27} = 5.703$, $P < 0.05$), lower leg length (LLL2; $F_{1,27} = 16.006$, $P < 0.001$), total leg length (TLL; $F_{1,27} = 13.532$, $P < 0.01$), cloacal length (CL; $F_{1,27} = 40.038$, $P < 0.001$), cloacal width (CW; $F_{1,27} = 50.601$, $P < 0.001$), upper arm diameter (UAD; $F_{1,27} = 21.346$, $P < 0.01$) and lower arm diameter (LAD; $F_{1,27} = 8.374$, $P < 0.01$).

The results of the MANOVA, with sex as a factor and morphometric characters as dependent variables, indicate that 12 out of 31 characters are sexually dimorphic in Near Eastern fire salamanders (table 3). Unlike the ANCOVA, SVL differed significantly between males and females in the MANOVA ($F_{1,28} = 4.386$, $P < 0.05$). SVL of females are larger than that of males, and SDI was calculated as 0.03, indicating a size dimorphism towards female-biased. What we consider at the most important dimorphic characters are shown in fig. 1.

Discussion

The results of this study indicate that sexual dimorphism of the Near Eastern fire salamander occurs not only in body size but also in body shape. Variation in sexual size and shape dimorphism may have significant effects on an organism's life-history traits, ecology, population dynamics and behavior. The equilibrium between sexual selection, fecundity selection and natural selection determines the strength of SSD (Fairbairn et al., 2007; Colleoni et al., 2014). SSD may occur between different species or between different populations and could be the consequence of different allometric patterns between the sexes (Butler & Losos, 2002; Labus et al., 2013).

In the studied population, *S. infraimmaculata* females are larger than males in terms of body size. Interestingly different results have been reported for sexual dimorphism within the genus *Salamandra*. For instance, Kalezić et al. (2000) revealed

Table 2.
Factor loadings for the principal components (PC; eigenvectors), eigenvalues and proportion of total variance described by the first three components obtained from PCA on a correlation matrix. Also shown are the F- and P-values of the ANCOVA with PC1 scores as covariate tests for differences in morphological variables.

Characters	PC1	PC2	PC3	F	P-value
SVL	0.774	−0.595	0.034	3.867	0.060
OAL	0.790	−0.501	0.267	1.463	0.237
TL	0.699	−0.346	0.448	0.176	0.678
TH	0.621	−0.003	0.036	2.833	0.104
UAL	0.650	0.358	0.112	10.321	<0.01
LAL	0.749	0.382	0.033	17.838	<0.001
LAL2	0.853	0.050	−0.094	5.185	<0.05
TAL	0.918	0.217	−0.019	11.864	<0.01
ULL	0.934	0.184	0.035	5.703	<0.05
LLL	0.722	0.237	−0.153	3.012	0.094
LLL2	0.725	0.549	−0.114	16.006	<0.001
TLL	0.690	0.563	−0.217	13.532	<0.01
CL	0.510	0.754	−0.271	40.038	<0.001
CW	0.485	0.805	−0.117	50.601	<0.001
CHW	0.305	0.417	0.315	2.930	0.098
BWM	0.503	0.327	0.532	2.200	0.150
PW	0.580	0.008	0.559	0.581	0.453
BL	0.845	−0.455	−0.008	0.488	0.491
UAD	0.814	0.386	0.120	21.346	<0.001
LAD	0.850	0.169	0.085	8.374	<0.01
ULD	0.398	−0.179	−0.440	0.039	0.845
LLD	0.664	−0.075	0.502	0.431	0.517
HL	0.720	−0.518	−0.105	1.825	0.188
HW	0.896	−0.149	−0.251	0.123	0.728
HD	0.832	−0.340	−0.255	0.198	0.660
ED	0.707	−0.422	−0.047	2.506	0.125
ON	0.728	−0.190	0.139	0.082	0.776
IO	0.913	−0.245	−0.145	0.105	0.749
IN	0.714	−0.179	−0.201	0.002	0.965
ES	0.581	−0.403	−0.296	1.405	0.246
IC	0.677	−0.002	−0.273	0.480	0.494
Eigen value	16.109	4.553	2.015		
% of variance	51.97%	14.69%	6.50%		
Cumulative %	51.97%	66.66%	73.16%		

that sexual dimorphism exists in *Salamandra salamandra* with males being larger than females. Contrasting with the study conducted by Kalezić et al. (2000), but being concordant with the general pattern of sexual size dimorphism for salamanders (Shine, 1979), Labus et al. (2013) reported that females are larger than males for

Table 3.
Results of the multivariate analysis of variance (MANOVA) in *S. infraimmaculata* for effects of the factor sex on the dependent variables. Only significant results are presented.

Dependent variable	df	Mean square	F	P-value
SVL	1	98.547	4.386	<0.05
UAL	1	3.535	11.166	<0.005
LAL	1	5.788	18.256	<0.001
LAL2	1	7.524	5.341	<0.05
TAL	1	19.417	10.394	<0.01
ULL	1	1.987	5.633	<0.05
LLL2	1	10.084	12.831	<0.001
TLL	1	10.580	12.560	<0.001
CL	1	8.466	41.141	<0.001
CW	1	2.857	54.186	<0.001
UAD	1	0.136	21.610	<0.001
LAD	1	0.036	8.382	<0.01

the same species. In the study of *Salamandra algira*, researchers analyzed 30 morphometric measures including body and head characters and they found no sexual dimorphism for overall body size (Reinhard et al., 2015).

Females are expected to be larger when there is a positive relationship between female size and fecundity (Shine, 1988). Fecundity selection is one of the most prevalent hypotheses advanced to explain why female amphibians are larger. However, irrespective of their reproductive mode (e.g., Gomez-Mestre et al., 2012; Han & Fu, 2013), many amphibians show sexual size dimorphism, and it is common that females are larger than males (Castanet et al., 2000; Olgun et al., 2005; Liao & Chen, 2012; Cadeddu et al., 2012; Altunışık & Özdemir, 2013; Liao, 2013; Liao et al., 2013b; Altunışık et al., 2014; Liao et al., 2015; Altunışık & Özdemir, 2015). According to the fecundity advantage hypothesis (Darwin, 1871; Shine, 1978), female-biased SSD is due to the selection favoring a large body size to ensure higher reproductive success, which also inverts Rensch's rule (Fairbairn, 1997; Liao et al., 2015). In additon to this hypothesis, sexual differences in life history traits (e.g. age structure and growth curve), ecology (niche partitioning between sexes), survival and sexual selection may also explain why females are bigger than males. Since we do not have the data to test the effect of ecological selection and fecundity selection, any of these hypotheses may explain the body size differences between sexes in the present study.

The arm length, arm diameter and limb length of *S. infraimmaculata* show sexual dimorphism, indicating that these characters are longer and larger in males than in females. Similarly in *Salamandra algira*, some morphometric characters (arm length and diameter, cloacal length and width) were sexually dimorphic towards a male-biased (Reinhard et al., 2015). In amphibian species that mate in an amplexus, it is common that male individuals have larger forelimbs and forelimb muscles than

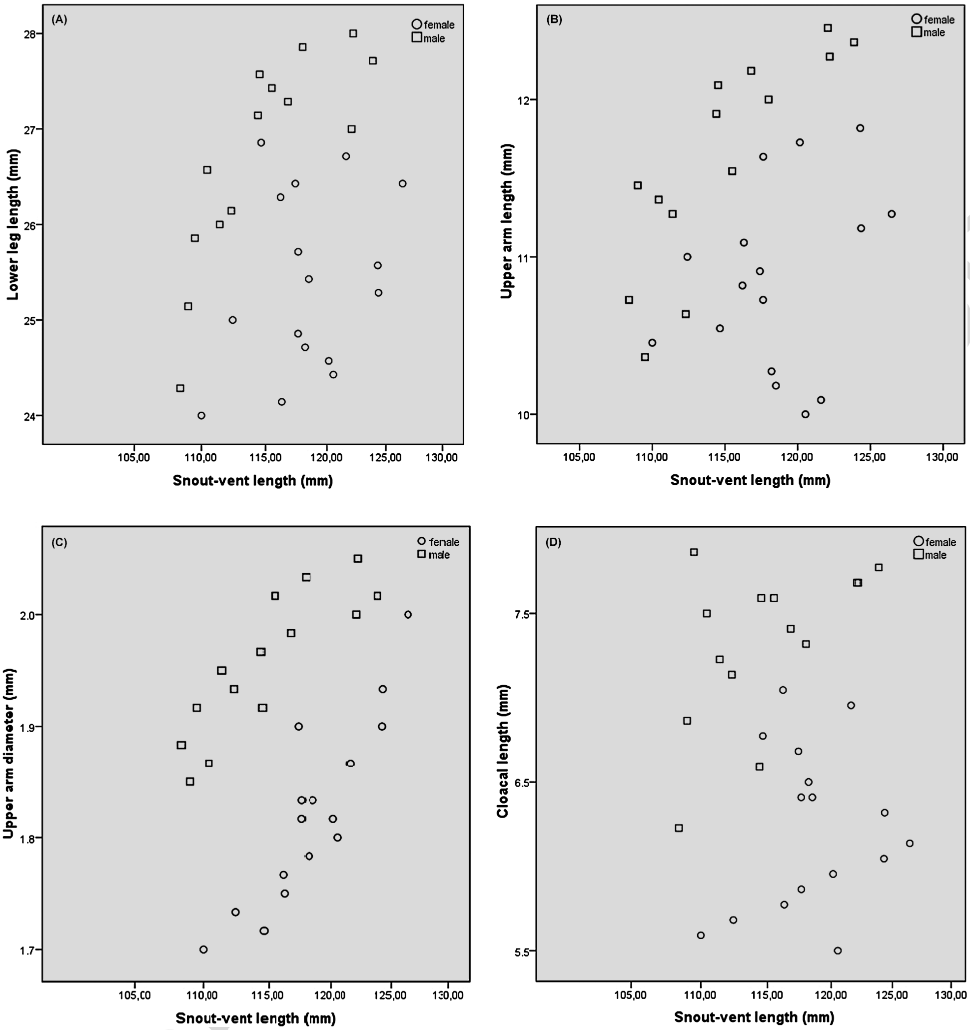

Figure 1. Sexual dimorphism of *Salamandra infraimmaculata* ($N = 16$ females and $N = 14$ males). Some selected dimorphic characters are shown: (A) lower leg length (LLL2); (B) upper arm length (UAL); (C) upper arm diameter (UAD); (D) cloacal length (CL). Males (□) have significantly larger sizes for each of these traits than females (○).

female (Wells, 2007). Since a male amphibian needs to grasps a female with his front legs as part of the mating process called amplexus, male individuals with enlarged forelimbs and muscles (especially adductor and flexor forelimb muscles: Peters & Aulner, 2000) are more successful in dominating females during mating and in preventing other males from interfering (reviewed in Reinhard et al., 2015). For instance, males of *Rhinella marina*, *Lithobates catesbeianus* and *Rana temporaria* have been reported to be successful in this sense (overview in Wells, 2007). The fact that male individuals of *S. infraimmaculata* have enlarged upper and lower arm diameter compared to female individuals also suggests that the adductor and flexor muscles of the forelimb may differ between female and male individuals. Since the larger male forelimbs of salamanders may provide advantage in male-male competition (e.g. male fighting and aggressive behavior; Zhang et al., 2014), mating success may be attributed to sexual selection (Bruce, 1993; Bakkegard & Guyer, 2004). In urodeles, 86.7% of species engage in male combat (Shine, 1979) and since females prefer larger males as their mate of choice, sexual selection favors males to have larger body size. However, there have been no reports about the mating system of *S. infraimmaculata*. Thus, further studies are needed to clarify if male combat occurs in *S. infraimmaculata*, and whether male-male competition can explain SSD in this salamander.

Cloacal body form is a notable and specific sexual trait that benefits male reproductive success, and results suggest that the structure of cloacal proportions (cloacal length and width) is also different in *S. infraimmaculata*, indicating a male-biased dimorphism. In accordance with the present study, Reinhard et al. (2015) reported that male S. *salamandra* had a larger cloacal length and width than females. However, females and males did not indicate significant differences in other characters such as body width, tail length, head size and eye diameter.

In summary, this study shows that both sexual size and shape dimorphism exist in *S. infraimmaculata*. Although females are slightly larger than males in terms of body size, males had higher values in the majority of the measured shape characters such as arm length, arm diameter, cloacal length and width. This sexual difference in morphological characters suggests that sexual selection favors mating success for these individuals. For a better understanding of size and shape dimorphism of this salamander, reproductive success of both males and females should now also be studied.

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Appendix

Table A1.
Descriptive statistics of morphometric characters of *S. infraimmaculata*.

Variables	Female ($N = 16$)		Male ($N = 14$)	
	Mean ± SE	Range	Mean ± SE	Range
SVL	118.52 ± 1.08	110.00-126.46	114.88 ± 1.38	108.40-123.87
OAL	203.67 ± 2.25	188.48-218.88	199.21 ± 2.72	185.93-215.59
TL	85.15 ± 1.31	76.01-94.16	84.33 ± 1.51	75.49-93.39
TH	9.22 ± 0.05	8.78-9.56	9.38 ± 0.08	8.91-10.15
UAL	11.19 ± 0.12	10.40-12.07	11.87 ± 0.16	10.76-12.71
LAL	11.73 ± 0.14	10.79-12.57	12.61± 0.14	11.57-13.32
LAL2	21.81 ± 0.31	19.22-23.42	22.82 ± 0.29	20.82-24.36
TAL	29.11 ± 0.31	26.73-31.15	30.73 ± 0.39	28.42-33.02
ULL	11.76 ± 0.14	10.81-12.78	12.27 ± 0.16	11.07-13.18
LLL	12.90 ± 0.11	11.99-13.62	13.18 ± 0.18	11.88-13.94
LLL2	25.45 ± 0.20	23.98-26.53	26.61± 0.25	24.30-27.84
TLL	31.60 ± 0.18	30.48-32.70	32.79 ± 0.28	30.12-34.16
CL	6.34 ± 0.10	5.68-7.10	7.40 ± 0.12	6.42-7.91
CW	2.55 ± 0.04	2.20-2.93	3.16 ± 0.07	2.64-3.52
CHW	21.59± 0.11	20.73-22.35	21.87 ± 0.10	21.12-22.62
BWM	20.32 ± 0.12	19.62-21.30	20.58 ± 0.06	20.10-20.87
PW	13.87 ± 0.17	12.62-15.10	14.07 ± 0.14	12.90-14.71
BL	69.33 ± 0.24	67.43-70.82	69.02 ± 0.29	67.31-70.67
UAD	1.83 ± 0.02	1.70-2.02	1.97 ± 0.02	1.85-2.10
LAD	1.70 ± 0.01	1.60-1.85	1.77 ± 0.01	1.69-1.87
ULD	2.66 ± 0.02	2.40-2.78	2.65 ± 0.05	2.00-2.87
LLD	2.32 ± 0.01	2.18-2.45	2.35 ± 0.02	2.19-2.58
HL	16.21 ± 0.13	14.72-16.72	15.86 ± 0.18	14.92-16.74
HW	20.45 ± 0.13	19.37-21.23	20.50 ± 0.15	19.17-21.31
HD	8.99 ± 0.07	8.29-9.30	8.92 ± 0.10	8.26-9.34
ED	1.68 ± 0.01	1.60-1.74	1.65 ± 0.01	1.58-1.72
ON	5.33 ± 0.02	5.17-5.55	5.34 ± 0.02	5.20-5.48
IO	12.78 ± 0.13	11.43-13.42	12.81 ± 0.17	11.50-13.70
IN	8.13 ± 0.07	7.43-8.52	8.12 ± 0.06	7.60-8.54
ES	9.59 ± 0.02	9.39-9.85	9.51 ± 0.05	9.20-9.86
IC	16.43 ± 0.02	16.23-16.56	16.45 ± 0.01	16.28-16.54