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Morphometric characterisation of a population of adult coconut crabs *Birgus latro* (Decapoda: Anomura: Coenobitidae) from Christmas Island in the Indian Ocean

Christiana Anagnostou[1*] & Christoph D. Schubart[2]

Abstract. Carapace and cheliped morphometry in sexually mature individuals of the coconut crab *Birgus latro* (Decapoda: Anomura: Coenobitidae) was analysed from six different locations on Christmas Island in the Indian Ocean in order to provide statistical evidence for heterochely and sexual dimorphism with regard to body size, cheliped size and heterochely. The absolute dimensions of weight, carapace length, cephalic shield length, thoracic length and width were significantly smaller in females than in males, confirming a pronounced sexual dimorphism in body size. For analysing intrasexual heterochely as well as sexual dimorphism with respect to cheliped size and heterochely, standardised values of the measured cheliped parameters corrected for size and allometric shape were used. For the allometric analyses of weight, and the cheliped propodus length and width, dactylus length, and merus length in relation to thoracic length, two statistical methods were applied and compared in order to identify the least error-prone method: A conventional linear Model II regression and a Model II non-linear analog of Reduced Major Axis Regression (RMA). Even though both methods resulted in the same pattern of allometry for the analysed parameters, the model fitted by the Model II non-linear analog of RMA regression mostly showed a better fit to the data. In both sexes, weight followed isometry. The cheliped parameters of females showed shallower allometric slopes than those of males. In both females and males, the dimension of the left cheliped parameters was significantly larger than that of the right (corresponding to the typical coenobitid heterochely), except for merus length in females. The standardised dimensions of the cheliped parameters as well as the degree of heterochely for all cheliped parameters were significantly larger in males than in females, providing evidence for a sexual dimorphism with respect to cheliped size and heterochely. Potential explanations for the evolution of heterochely and sexual dimorphism in *B. latro* are discussed.

Key words. morphometry, allometry, heterochely, sexual dimorphism, sexual selection, intersexual niche divergence

INTRODUCTION

“These monstrous crabs have a mixed shape, that of a Crab and a Crayfish… It has two very powerful pincers, of which one, usually the right one, is smaller than the other…”, the Dutch naturalist G. E. Rumphius (1705) writes in one of the first detailed descriptions of *Birgus latro* (Linnaeus, 1767). This world’s largest land-living arthropod is commonly referred to as robber crab or coconut crab and is a representative of the superfamily of hermit crabs (Paguroidea), most of whose members are well known for carrying empty shells (mainly gastropod shells) for protection. Within the family of terrestrial hermit crabs (Coenobitidae), *B. latro* is the least marine-dependent representative (Greenaway, 2003), and monotypic within its genus (Helfman, 1979). With a thoracic length of approximately 8–10 mm, juvenile *B. latro* abandon their shell and migrate to terrestrial habitats (Brown & Fielder, 1991; Drew et al., 2010). *B. latro* is widely distributed mainly on isolated and remote tropical islands throughout the Indian and western Pacific oceans, ranging from islands near Zanzibar/Tanzania in the Indian Ocean to the Gambier Islands/French Polynesia in the Pacific (Lavery et al., 1996). Almost throughout their entire range, coconut crabs are highly sought after for their meat. Due to intensive harvesting for human consumption (Fletcher, 1993), but also as a consequence of habitat destruction (Eldredge, 1996), crab populations are declining (Brown & Fielder, 1991). In 1981, *B. latro* was listed as a vulnerable species on the International Union for Conservation of Nature (IUCN) Red List, but due to a lack of available data, it has been reassessed as “Data Deficient” since 1996 (Eldredge, 1996). On Christmas Island (CI) in the Indian Ocean, *B. latro* is a protected species within the National Park (EPBC Regulations 2000, Schedule 12) which comprises approximately 63% of the island (Christmas Island National Park Draft Management Plan 2012–2022, 2012). The population of *B. latro* on CI is reported to be very large compared to other islands within the Indo-Pacific inhabited by the species. Despite the fascination it has long exerted on explorers, sailors and naturalists (Drake, 1628; Rumphius, 1705; Darwin, 1845), there is still

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"a lack of systematic research even on the basic biology of the species" (Drew et al., 2010). A lot of information on life history aspects of *B. latro* is of "anecdotal nature" (Fletcher, 1993) or "based on brief observations and thus lacks rigour" (Drew et al., 2010).

The aim of this study was to gather large datasets of morphometric values and to provide statistical evidence for the observations that sexually mature individuals of *B. latro* exhibit heterochely and sexual dimorphism with regard to body size, cheliped size, and heterochely. The corresponding statistical H_0 hypotheses tested were: (i) There is no difference in the standardised dimensions of the measured cheliped parameters (corrected for size and allometric shape) of the left and right cheliped in both females and males. (ii) There is no difference in the dimensions of the measured body size parameters between females and males. (iii) There is no difference in the standardised dimensions of the measured cheliped parameters between females and males. (iv) There is no difference in the degree of heterochely of the measured cheliped parameters between females and males. In order to analyse the degree of intrasexual and intersexual heterochely, we calculated standardised values of the measured cheliped parameter dimensions, corrected for both size and allometric shape (Lleonart et al., 2000). Standardisation was based on the state of allometry characterised for the cheliped parameters in relation to the body size parameter thoracic length in both sexually mature female and male individuals. In answer to the criticism uttered by Zar (1968) and Packard (2012) on the errors associated with the conventionally used allometric method of fitting a straight line to logarithmic transformations of the investigated variables and subsequent retransformation to a power function, we applied and compared two different statistical methods for the allometric growth analyses in order to identify the least error-prone method: A conventional linear Model II regression on logarithmically transformed values of the measured parameters, using either Reduced Major Axis Regression or Major Axis Regression, and a Model II non-linear analog of Reduced Major Axis Regression on non-transformed values (Ebert & Russel, 1994).

MATERIAL AND METHODS

Study site. Christmas Island (10°30'S, 105°40'E), external territory of the Commonwealth of Australia since 1958, comprises an area of about 135 km² and is located in the Indian Ocean, approximately 360 km south of Java, Indonesia, and 2600 km northwest of Perth on the Australian mainland (Fig. 1A). It originated from an approximately 47 million year old seamount recycled rock from the ancient supercontinent Gondwana and has experienced repeated uplifts and submersions (Hoernle et al., 2011). The island's landmass is characterised by staggered plateaus separated by rugged cliffs and rises steeply from a coastal and middle plateau to a central plateau of up to 361 m. The soils of the island are derived from limestone (uplifted former coral reefs) and basaltic (volcanic) rock. Due to the porous limestone rocks the island lacks permanent surface water, despite its high mean annual rainfall of 2000 mm. Fresh water merely reaches the surface in areas with basaltic rock, where perennial streams occur, such as at The Dales, Hosnie's Springs, and Dolly Beach (Fig. 1B). Most of the island is covered by tropical rain forest, including endemic species like *Pandanus elatus* and *Arenga listeri*. Christmas Island's climate is tropical and oceanic with a wet season, usually from December to April, and a dry season from May to November. *Birgus latro* is distributed throughout the island.

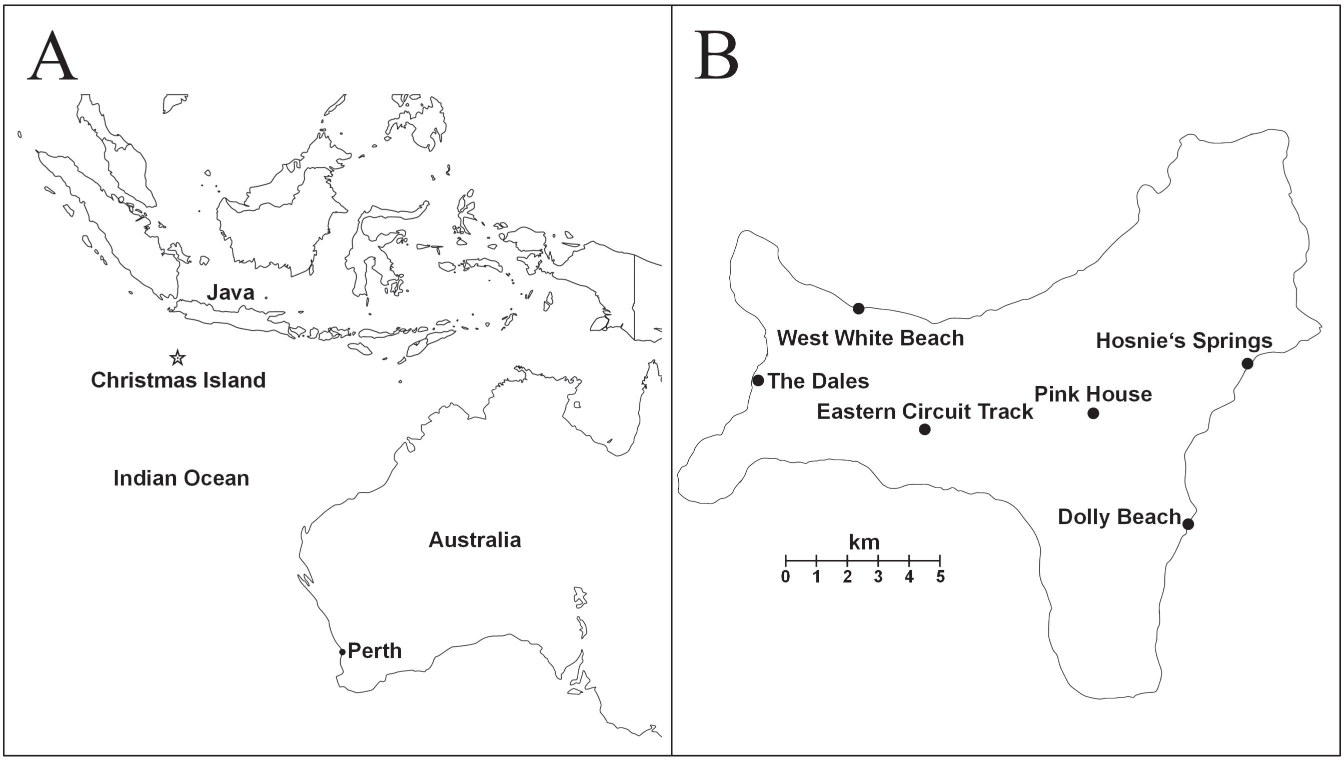

Fig. 1. A, Location of Christmas Island in the Indian Ocean (modified after www.freemap.jpg). B, Map of Christmas Island showing the locations where *Birgus latro* was sampled (black circles).

Sampling. This field study was carried out during dry season in August and early September 2012. Sampling was conducted with permission from Christmas Island National Park (Parks Australia North permit number AU-COM2012-140). A total of 120 sexually mature individuals of *Birgus latro* were hand-caught during both day and night time at six different locations: Eastern Circuit Track (ECT), Dolly Beach (DB), Hosnie's Springs (HS), Pink House (PH), The Dales (TD), and West White Beach (WWB) (Fig. 1B). Several different sampling locations were preferred over a single sampling location in order to obtain a more representative sample of the whole population on Christmas Island. Additionally, we aimed to investigate potential differences in morphometry and genetics (microsatellite markers) among individuals from different locations (not part of this publication). Sex was recognised by the presence (female) or absence (male) of pleopods (three biramous setaceous appendages on the left side of the abdomen). Based on a study of Sato & Yoseda (2008), as well as Sato et al. (2008), female and male individuals of a thoracic length of >25 mm were considered to be sexually mature. Thus, all sampled individuals had to fulfill the prerequisite of having a TL of >25 mm. Other than that, individuals were sampled randomly. The following morphometric measures of the carapace and the major left (L) and minor right (R) chelipeds were taken using Digimatic digital calipers (precision +/– 0.04 mm): carapace length (CL), cephalic shield length (CSL), thoracic length (TL), thoracic width (TW) (Fig. 2A), cheliped propodus length (CPL), cheliped propodus width (CPW), cheliped dactylus length (CDL), and cheliped merus length (CML) (Fig. 2B). The crabs' weight (W) was determined with a Kern & Sohn HDB 5K5N digital hanging scale (precision +/– 5 g). All sampled crabs were marked with a black waterproof marker (STAEDTLER) on their dorsal carapace to avoid subsequent resampling within the following days, and were released at the site of capture. According to investigations made prior to sampling, the marker remained clearly visible for at least eight weeks.

Statistical analyses. All statistical analyses were carried out with R 2.15.2, except for the Model II non-linear analog of Reduced Major Axis Regression analyses which were carried out with SPSS 20.

Dimensions of body parameters. The difference in female and male body parameters was analysed by applying either independent sample t-tests, in the case of parametric data, or independent sample Wilcoxon rank sum (Mann-Whitney) tests, in the case of non-parametric data or presence of distinctive outliers. Shapiro-Wilk tests for analysing normality of data as well as Levene's tests for analysing homogeneity of variances were applied to test whether data was parametric. The means of female and male body parameters were used to calculate a compressed size dimorphism index (SDI) as introduced by Lovich & Gibbons (1992), and supported by Smith (1999) as well as Fairbairn et al. (2007). The SDI is calculated by dividing the mean size of the larger sex (here males) by the mean size of the smaller sex (here females),

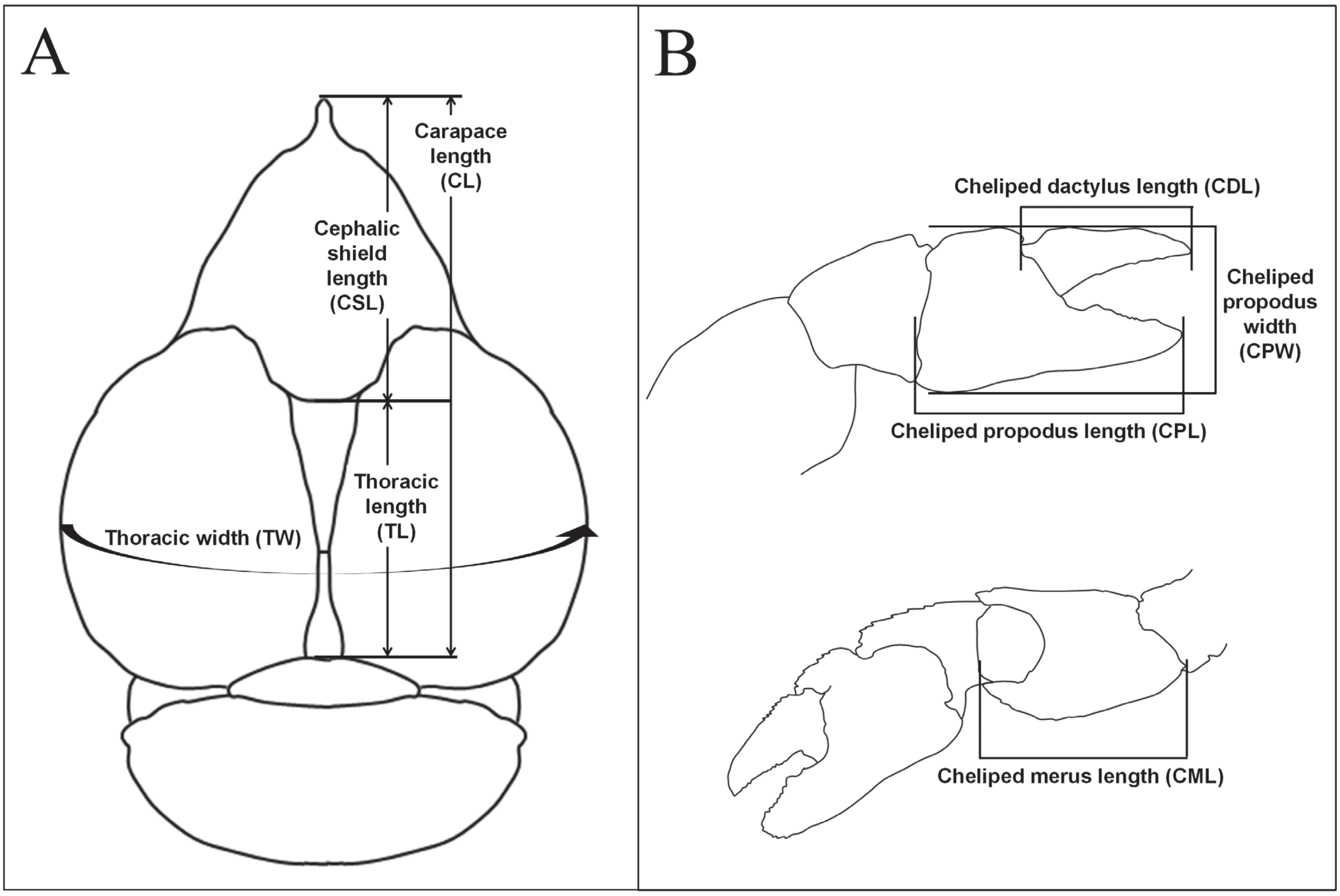

Fig. 2. Morphometric carapace and cheliped parameters measured in female and male *Birgus latro*. A, Carapace parameters shown on the dorsal side of the crab. B, Cheliped parameters shown on the dorsal (top) and ventral side (bottom) of the right cheliped.

and subtracting one from this value, which sets the neutral value (i.e., when females and males are of equal size) to zero rather than one. Arbitrarily, the resulting value of SDI additionally renders a negative value when males are larger than females, and a positive value when females are larger than males. Thus, for *B. latro* the SDI was calculated as: $-[(\text{size}_{\text{males}}/\text{size}_{\text{females}}) - 1]$. The degree of size dimorphism (SD) was calculated as SD [%] = ABS(SDI)*100.

Allometric growth analyses. In the allometric growth analyses, weight as well as dimensions of the left and right cheliped parameters (LCPL & RCPL, LCPW & RCPW, LCDL & RCDL, LCML & RCML) (dependent variables) were related to thoracic lengt as reference dimension (independent variable). TL was preferred to carapace length, cephalic shield length, as well as thoracic width, since it is the linear measurement which is least prone to both measuring errors and variation due to injuries in the crabs, such as a damaged rostrum (Amesbury, 1980). All allometric growth analyses were based on the allometric equation $y = a*x^b$ (y: dependent variable, x: independent variable, a: shape parameter as intercept on the y-axis, b: allometric growth coefficient) and its natural logarithmic transformation $\ln y = \ln a + b*\ln x$, where the allometric growth coefficient b is the slope in this linear equation (Huxley, 1950; Hartnoll, 1978, 1982, 1985). We applied and compared two different statistical methods for the allometric growth analyses. (i) A conventional linear Model II regression (used when the two variables in the regression equation are random rather than fixed), with either using Reduced Major Axis Regression (RMA) for W versus TL (variables not expressed in the same physical units) or Major Axis Regression (MA) for the cheliped parameters versus TL (both variables expressed in the same physical units). (ii) Non-linear regression with a Model II non-linear analog of RMA Regression as presented by Ebert & Russel (1994). Instead of a loss function based on the minimisation of deviations only in the dependent variable y, we applied the following loss function, which also considers the independent variable x to be subject to errors and has been developed by Ebert & Russel (1994):

ABS(y*ABS(x–(y/a)^(1/b))–a/(b+1)*ABS(x^(b+1)–(y/a)^((b+1)/b)))

The allometric growth analyses were carried out for the values of females and males separately.

Allometric growth analysis using linear Model II regression

After plotting the natural logarithms of the dependent (LCPL & RCPL, LCPW & RCPW, LCDL & RCDL, LCML & RCML, W) and independent variable (TL), their relationship was described by the linear equation resulting from a linear Model II regression:

ln dependent variable = ln a + b * ln independent variable

The state of allometry of each cheliped parameter and weight was determined by checking whether b=3 (for weight) or b=1 (for the cheliped parameters) falls into the 95% confidence intervals computed by the linear Model II regression (H_0: b=3 & H_1: b≠3 and H_0: b=1 & H_1: b≠1, respectively). In case b=3 or b=1 did not fall into the 95% confidence interval and b>3 or b>1, growth was considered to be positively allometric. In case b=3 or b=1 did not fall into the 95% confidence interval and 0<b<3 or 0<b<1, growth was considered to be negatively allometric. In case b=3 or b=1 fell into the 95% confidence interval, growth was considered to be isometric.

Allometric growth analysis using non-linear regression

A non-linear regression was carried out on the original (i.e., not logarithmically transformed) bivariate data, using the loss function shown above. The non-linear regression directly computes estimations for the parameters a and b of the allometric equation $y = a*x^b$. The state of allometry was determined in analogy to the method described above, based, however, on the confidence intervals computed by the non-linear regression via a Bootstrap procedure.

Standardisation of cheliped parameters. In order to achieve a size and shape independent comparison of the size of the cheliped parameters between females and males, as well as to remove the effect of size and shape on the morphological analysis of heterochely, the absolute values of the cheliped parameters were standardised as proposed by Lleonart et al. (2000). The absolute measurements were converted by using the equation: $Y_i^* = Y_i*(X_0/X_i)^b$, with Y_i^* representing the standardised value of the cheliped parameters LCPL & RCPL, LCPW & RCPW, LCDL & RCDL, LCML & RCML, Y_i the individual absolute value of the cheliped parameters, X_0 the mean absolute value of TL, X_i the individual absolute value of TL, and b the slope of the allometric equation resulting from the non-linear regression carried out on the separate values of females and males. This standardisation was preferred to merely calculating the ratio between the respective cheliped parameter and TL, since apart from setting all individuals to the same size, it also considers the individuals' different allometric shapes (Lleonart et al., 2000).

Dimensions of cheliped parameters and heterochely. The difference in dimension of the absolute as well as the standardised cheliped parameters between females and males was analysed by applying independent sample Wilcoxon rank sum (Mann-Whitney) tests. The degree of heterochely in both females and males was described by calculating an asymmetry index (AI) as proposed by Van Valen (1962): $AI = (R^*-L^*)/(R^*+L^*)$, with R^* and L^* representing the standardised values of the measured parameters of the right (R) and left (L) chelipeds. The values of AI range between –1 and +1. If AI is 0, there is no difference in the measured dimension between the right and left cheliped parameter (perfect homochely). If AI is smaller than 0, the dimension of the left cheliped parameter is larger than that of the right cheliped parameter (heterochely). If AI is larger than 0, the dimension of the left cheliped parameter is smaller than that of the right cheliped parameter (heterochely). Differences in median AI values between females and males were tested by applying independent sample Wilcoxon rank sum (Mann-Whitney) tests. Significant deviations of median AI values from zero were analysed by applying one-sample Wilcoxon-tests.

Table 1. Number of male and female *Birgus latro* sampled at the different locations on Christmas Island, as well as the range of the absolute dimensions of thoracic length (TL) and weight (W) of the sampled individuals. n = number of individuals.

	Sampling locations						**Total**
	Dolly Beach	**Eastern Circuit Track**	**Hosnie's Springs**	**Pink House**	**The Dales**	**West White Beach**	
n_{total}	22	22	22	26	24	4	120
$n_{females}$	1	12	10	11	10	2	46
n_{males}	21	10	12	15	14	2	74
TL [mm] in females	44.41–44.41	39.17–46.82	45.32–50.33	39.72–48.95	36.60–47.03	46.36–48.09	36.60–50.33
TL [mm] in males	59.00–68.96	59.89–69.36	55.54–72.52	59.60–71.14	57.11–69.04	57.88–67.50	55.54–72.52
W [g] in females	785–785	525–755	620–945	560–970	465–730	895–975	465–975
W [g] in males	1800–2655	1585–2405	1420–2750	1475–2455	1590–2260	1355–2465	1355–2750

RESULTS

Sampling. Table 1 summarises the total number of individuals as well as the number of female and male *Birgus latro* that were sampled at the different locations. The number of encountered individuals differed between the locations. At WWB, e.g., merely four individuals could be found. Therefore, ECT was subsequently chosen as an additional sampling location. The proportion of encountered females and males also differed between the locations. For example, at DB only a single female was found. The time of day at which the crabs were active and could be sampled, also differed between the locations. While crabs were active and easily spotted during daylight hours at DB, HS and TD, active crabs at ECT, PH, and WWB could mainly be encountered and sampled during the night. None of the encountered or sampled females carried eggs.

Dimensions of body parameters and sexual size dimorphism. The absolute dimensions of the body parameters weight, carapace length, cephalic shield length, thoracic length as well as thoracic width of females were significantly smaller than those of males (with no overlap recorded), thus indicating a pronounced sexual size dimorphism and rejection of H_0 (ii) (Fig. 3 and Table 2, boxplot in Fig. 5). Regarding CL, CSL, TL and TW, sexes differed by approximately 42%, and regarding W by 198%. The range in TL as well as the range in W of female and male individuals from the six different locations are shown in Table 1. The average size difference in TL between the sexes was 19.68 ± 6.87 mm (mean ± standard deviation). The average difference in W between the sexes was 1362 ± 435 g (mean ± standard deviation). During sampling, no sexually mature male with a TL below 55.5 mm, and no sexually mature female with a TL below 36.6 mm were encountered.

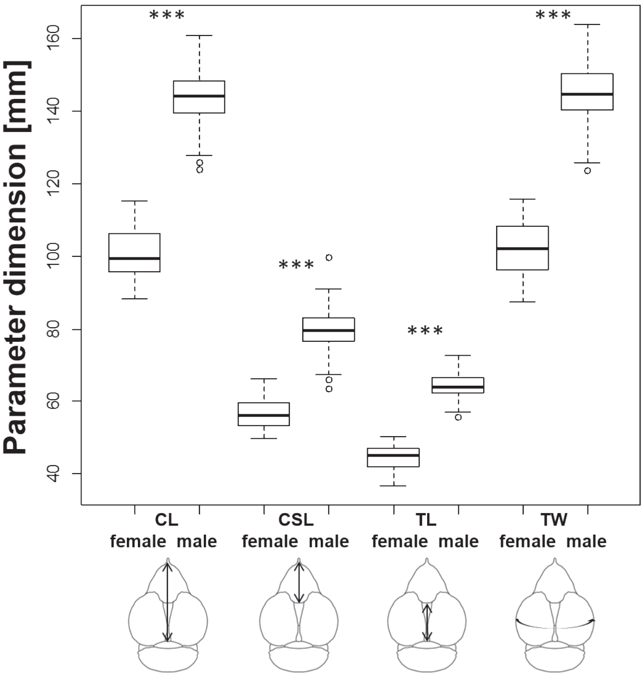

Fig. 3. Absolute dimensions of body parameters of female and male *Birgus latro*. Parameters: CL = carapace length, CSL = cephalic shield length, TL = thoracic length, TW = thoracic width. *** indicates $p < 0.001$.

Allometric growth. Generally, the linear Model II regression resulted in the same state of allometry for weight and the measured cheliped parameters in relation to thoracic length as the Model II non-linear regression (Figs. 4 & 5 and Table 3). However, the model fitted by the Model II non-linear analog of RMA regression mostly showed a better fit to the data than the model fitted by the linear Model II regression. In both sexes, weight followed isometry. In females, the cheliped parameters LCPL/RCPL, LCPW/RCPW and LCDL/RCDL showed isometry, and LCML/RCML negative allometry.

Table 2. Summary of the absolute dimensions of body parameters in female and male *Birgus latro*, given as mean ± standard deviation (sd), the results of the independent sample t-tests and Wilcoxon rank sum (Mann-Whitney) tests, respectively, as well as the sexual dimorphism index (SDI) for each of the parameters. Parameters: W = weight, CL = carapace length, CSL = cephalic shield length, TL = thoracic length, TW = thoracic width.

Parameter	Sex	Parameter value ± sd	Result of Wilcoxon rank sum test/ independent sample t-test	SDI
W	Females	687 ± 136 g	W = 0, p-value < 0.001	–1.98
	Males	2049 ± 299 g		
CL	Females	101.00 ± 7.33 mm	t = –29.9818, df = 117, p-value < 0.001	–0.42
	Males	143.90 ± 7.76 mm		
CSL	Females	56.54 ± 4.46 mm	W = 7, p-value < 0.001	–0.41
	Males	79.72 ± 5.62 mm		
TL	Females	44.49 ± 3.44 mm	t = –30.5018, df = 118, p-value < 0.001	–0.44
	Males	64.17 ± 3.44 mm		
TW	Females	102.30 ± 7.69 mm	t = –26.8467, df = 115, p-value < 0.001	–0.41
	Males	144.70 ± 8.70 mm		

Table 3. Linear Model II regression parameters (intercept e^{lna} and slope b), non-linear regression parameters (intercept a and slope b) of a Model II non-linear analog of Reduced Major Axis Regression with the loss function as proposed by Ebert and Russel (1994), 95 % confidence interval (95% CI), and state of allometry of left and right cheliped parameters as well as weight (W) (dependent variables) against thoracic length (TL) (independent variable) in male and female *Birgus latro*. Parameters: LCPL = left cheliped propodus length, LCPW = left cheliped propodus width, LCDL = left cheliped dactylus length, LCML = left cheliped merus length, RCPL = right cheliped propodus length, RCPW = right cheliped propodus width, RCDL = right cheliped dactylus length, RCML = right cheliped merus length. Par = parameter, n = number of individuals, r^2 = coefficient of determination for the linear Model II regression, lr = linear Model II regression, nlr = Model II non-linear analog of Reduced Major Axis Regression. State of allometry: – = negative allometry, 0 = isometry, + = positive allometry.

Sex	Par	n	Allometric equation $Par=e^{lna}*TL^b$	r^2	Allometric equation $Par=a*TL^b$	95% CI for slope b		State of allometry	
						lr	nlr	lr	nlr
Female	LCPL	46	$Par=1.684*TL^{0.957}$	0.47	$Par=1.385*TL^{1.009}$	0.688–1.325	0.781–1.236	0	0
	LCPW	46	$Par=0.256*TL^{1.326}$	0.46	$Par=0.333*TL^{1.256}$	0.963–1.884	0.986–1.526	0	0
	LCDL	46	$Par=0.480*TL^{1.146}$	0.43	$Par=0.474*TL^{1.149}$	0.808–1.654	0.853–1.445	0	0
	LCML	45	$Par=2.964*TL^{0.743}$	0.57	$Par=2.217*TL^{0.819}$	0.559–0.966	0.695–0.943	–	–
	RCPL	46	$Par=1.738*TL^{0.908}$	0.66	$Par=1.527*TL^{0.942}$	0.727–1.128	0.800–1.084	0	0
	RCPW	46	$Par=0.857*TL^{0.951}$	0.67	$Par=0.749*TL^{0.987}$	0.765–1.179	0.838–1.136	0	0
	RCDL	46	$Par=0.654*TL^{1.033}$	0.65	$Par=0.619*TL^{1.048}$	0.825–1.297	0.907–1.190	0	0
	RCML	45	$Par=3.004*TL^{0.743}$	0.71	$Par=2.572*TL^{0.779}$	0.559–0.966	0.669–0.890	–	–
	W	46	$Par=0.036*TL^{2.598}$	0.80	$Par=0.031*TL^{2.635}$	2.236–3.045	2.254–3.017	0	0
Male	LCPL	74	$Par=0.173*TL^{1.543}$	0.41	$Par=0.486*TL^{1.300}$	1.178–2.105	1.057–1.542	+	+
	LCPW	74	$Par=0.137*TL^{1.474}$	0.33	$Par=0.329*TL^{1.264}$	1.072–2.115	1.071–1.457	+	+
	LCDL	74	$Par=0.003*TL^{2.384}$	0.22	$Par=0.028*TL^{1.866}$	1.615–4.086	1.713–2.020	+	+
	LCML	74	$Par=0.539*TL^{1.169}$	0.53	$Par=0.704*TL^{1.106}$	0.937–1.471	0.924–1.287	0	0
	RCPL	73	$Par=0.450*TL^{1.249}$	0.48	$Par=0.690*TL^{1.146}$	0.982–1.610	0.902–1.391	0	0
	RCPW	73	$Par=0.163*TL^{1.366}$	0.47	$Par=0.295*TL^{1.224}$	1.069–1.781	1.014–1.434	+	+
	RCDL	73	$Par=0.115*TL^{1.456}$	0.31	$Par=0.302*TL^{1.225}$	1.035–2.152	1.023–1.426	+	+
	RCML	73	$Par=0.765*TL^{1.078}$	0.59	$Par=0.880*TL^{1.044}$	0.883–1.319	0.918–1.169	0	0
	W	74	$Par=0.006*TL^{3.067}$	0.65	$Par=0.022*TL^{2.749}$	2.599–3.670	2.471–3.026	0	0

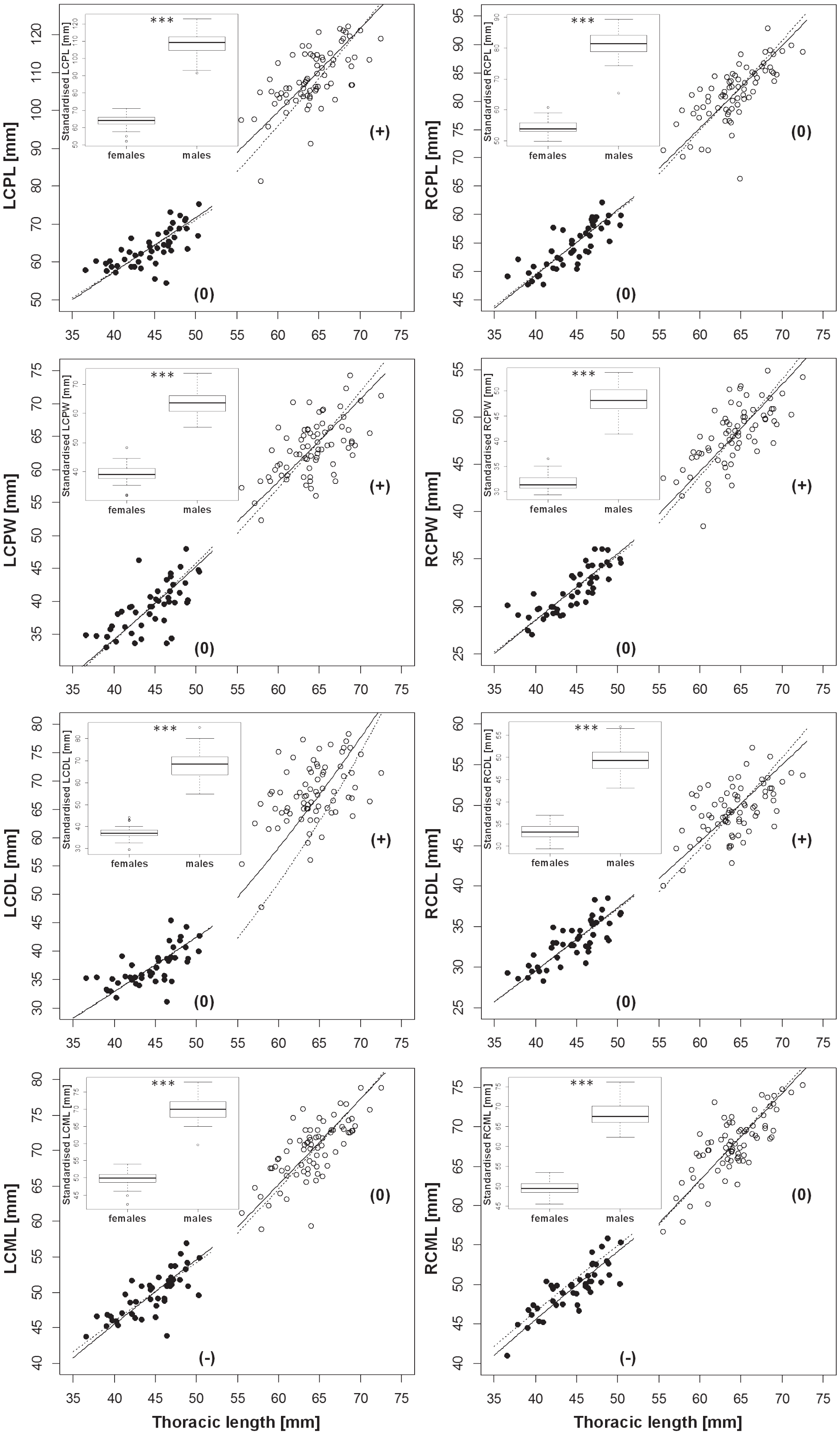

Fig. 4. Boxplots of the standardised cheliped parameters of female and male *Birgus latro*, as well as scatterplots of the cheliped parameters in relation to thoracic length, including the fitted curves of the linear Model II regression (dotted lines) and the Model II non-linear analog of a Reduced Major Axis regression (solid lines). Parameters: LCPL = left cheliped propodus length, RCPL = right cheliped propodus length, LCPW = left cheliped propodus width, RCPW = right cheliped propodus width, LCDL = left cheliped dactylus length, RCDL = right cheliped dactylus length, LCML = left cheliped merus length, RCML = right cheliped merus length. Filled circles in the scatterplot indicate values of females, open circles indicate values of males. The symbols in brackets indicate the state of allometry: (–) = negative allometry, (0) = isometry, (+) = positive allometry. *** indicates $p < 0.001$.

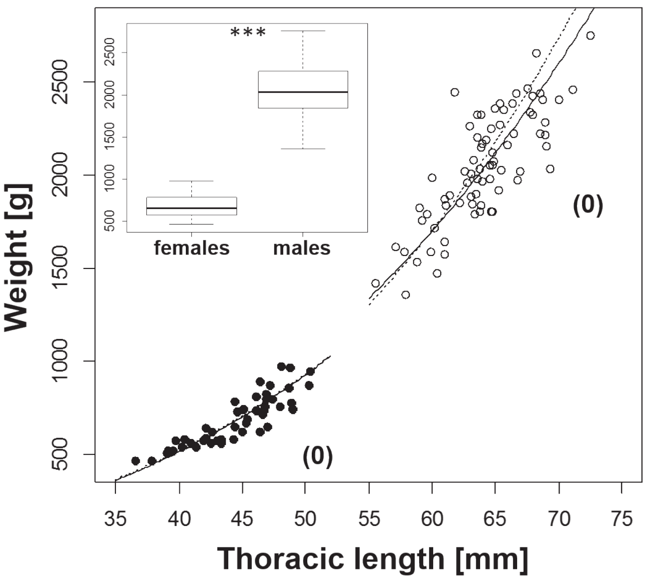

Fig. 5. Boxplot of the absolute weight of female and male *Birgus latro*, as well as scatterplot of weight in relation to thoracic length, including the fitted curves of the linear Model II regression (dotted lines) and the Model II non-linear analog of a Reduced Major Axis regression (solid lines). Filled circles in the scatterplot indicate values of females, open circles indicate values of males. The symbols in brackets indicate the state of allometry: (0) = isometry. *** indicates $p < 0.001$.

In males, LCPL, LCPW/RCPW and LCDL/RCDL showed positive allometry, and RCPL and LCML/RCML isometry.

Dimensions of cheliped parameters and heterochely. Apart from one male individual whose right cheliped was missing, all sampled individuals showed intact chelipeds and no unusually small limbs, which may indicate regeneration after loss. Corresponding to body size, the absolute dimensions of the cheliped parameters LCPL & RCPL, LCPW & RCPW, LCDL & RCDL and LCML & RCML of females were significantly smaller than those of males ($W = 0$, $p < 0.001$, for all comparisons). When comparing the standardised dimensions of the cheliped parameters corrected for size as well as allometric shape, female cheliped parameters were significantly smaller than those of males ($W = 0$, $p < 0.001$, for all comparisons), indicating a pronounced sexual dimorphism with regard to the cheliped parameters and rejection of H_0 (iii) (boxplots in Fig. 4). In females, there was a significant difference of the asymmetry index (AI) values from zero for all measured cheliped parameters except CML (CPL: $V = 0$, $p < 0.001$; CPW: $V = 0$, $p < 0.001$; CDL: $V = 2$, $p < 0.001$; CML: $V = 442$, $p = 0.401$) (Fig. 6). Thus, the size of the left cheliped parameter was significantly larger than that of the right one for all measured cheliped parameters, except for CML (rejection of H_0 (i), except for CML). In males, the AI values of all measured cheliped parameters differed significantly from zero (CPL: $V = 0$, $p < 0.001$; CPW: $V = 0$, $p < 0.001$; CDL: $V = 0$, $p < 0.001$; CML: $V = 134$, $p < 0.001$), i.e., for all measured cheliped parameters the size of the left cheliped parameter was significantly larger than th of the right one (rejection of H_0 (i)). For each of the measured cheliped parameters, a significant difference in the AI values between female and male *B. latro* was found (CPL: $W = 325$, $p < 0.001$; CPW: $W = 270$, $p < 0.001$; CDL: $W = 330$, $p < 0.001$; CML: $W = 256$, $p < 0.001$). Thus, the degree of heterochely was significantly larger in males than in females, indicating a pronounced sexual dimorphism with regard to heterochely (rejection of H_0 (iv)).

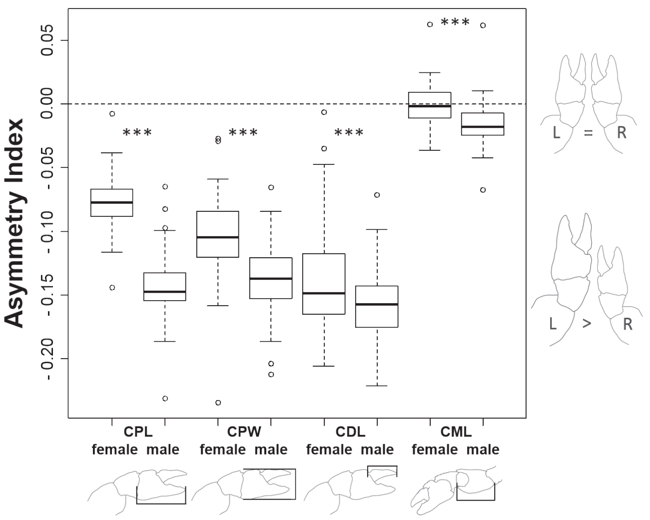

Fig. 6. Asymmetry index of female and male *Birgus latro* for the measured cheliped parameters. The dashed line indicates the asymmetry index of zero with no difference in the measured dimension between the right and left cheliped parameter (perfect homochely). Parameters: CPL = cheliped propodus length, CPW = cheliped propodus width, CDL = cheliped dactylus length, CML = cheliped merus length. *** indicates $p < 0.001$.

DISCUSSION

Size range of individuals encountered during sampling. One striking phenomenon during the sampling was the rarity of individuals of *Birgus latro* with a thoracic length <55.5 mm (males), and <36.6 mm (females). Apart from chance effects, a potential reason may be that sampling was carried out during dry season. Smaller individuals are more prone to desiccation than larger ones (unfavourable surface to volume ratio) and may have thus stayed in their burrows. Another potential explanation might be that successful recruitment events in *B. latro* are reported to take place only every five to ten years (Drew et al., 2010 and references therein). Rumpff (1986, in Drew et al., 2010) had already noted distinct “gaps” in the size-frequency classes of female and male *B. latro* on Christmas Island, suggesting the size classes to represent different generations. He proposed that infrequent successful spawning events may be responsible for this.

Sexual dimorphism. Sexual dimorphism (SD), defined as the morphological differentiation of sexually mature females and males (Fairbairn, 1997), is assumed to have evolved through sexual selection (female choice, intrasexual competition), fecundity selection, and/or intersexual niche divergence (Darwin, 1871; Shine, 1989; Andersson, 1994). One of the most easily recognised forms of SD is sexual size dimorphism (SSD), the difference in adult body size between females and males, resulting from sex-specific differences in growth rate and growth duration (Badyaev, 2002; Allen et al., 2011).

SSD with males being larger than females occurs in many species of hermit crabs (Contreras-Garduño & Córdoba-Aguilar, 2006), and all morphological studies of *Birgus latro* (including the present one) have found this species to exhibit a pronounced SSD (Fletcher et al., 1991b; Fletcher, 1993; Drew et al., 2010). The average difference in TL between females and males of 19.68 ± 6.87 mm (mean ± standard deviation) found in our study, is very similar to the average difference in TL found in former studies, with 21.9 ± 7.7 mm (Drew et al., 2010 and references therein). Regarding TL, the compressed size dimorphism index SDI was –0.44, regarding weight it was –1.98. In comparison, the SDI of the southern elephant seal *Mirounga leonina*, which exhibits an extreme SSD, can be as large –0.73 regarding body length and –5.98 regarding weight (based on values in Lindenfors et al., 2002). Sexual selection (mate choice and intrasexual competition) is the selective force most agreed upon by evolutionary biologists driving the evolution of especially male-biased SSD (males > females). In mammalian taxa, it is mostly the largest sized taxa which exhibit the greatest SSD, due to intense sexual competition (Weckerly, 1998). In studies on several decapod crustaceans, larger males were shown to be preferred by females (female mate choice), and to win contests against smaller males for access to females (male-male competition) (Aquiloni & Gherardi, 2008; Hunt et al., 2009 and references therein; Robertson & Butler, 2013). In studies on hermit crabs, there is more support for SSD being related to direct competition among males than to female mate choice (Contreras-Garduño & Córdoba-Aguilar, 2006 and references therein). The study of Sato & Yoseda (2010) on *B. latro* from Hatoma Island suggests that females prefer to mate with males that are larger or approximately equal to them in size. Additionally, large males showed a higher reproductive potential compared to small males, which might be one factor responsible for the preference of females for large males: Large males were able to pass more sperm to females even with increasing male mating frequency, females showed a higher fertilisation rate when mated with large males, and the number of spermatozoa in the vasa deferentia and testes, as well as spermatophore volume, was shown to increase with increasing male body size (Sato et al., 2008, 2010; Sato, 2011). Thus far, there are no studies on sexual selection regarding male-male competition in *B. latro*. Even though agonistic behaviour between males has repeatedly been described (Helfman, 1973; Amesbury, 1980; personal observation), it is not clear whether this is connected with competition for access to females.

An alternative explanation for the evolution of SSD is fecundity selection (Darwin, 1871; Andersson, 1994; Allen et al., 2011). In many invertebrates, fish and birds, the evolution of female-biased SSD (females > males) has been proposed to be conferred via fecundity selection, where fecundity in females may increase with increasing body size (Stillwell et al., 2010). The applicability of this fecundity-advantage explanation may, however, be determined by energy constraints causing a trade-off between growth and reproduction (Shine, 1988). Larger females of *B. latro* have been shown to produce offspring with larger body size and weight and longer survival periods under non-fed conditions compared to females of smaller body size (Sato & Suzuki, 2010). The SSD in *B. latro* is, however, male-biased. Together with the findings that females prefer to mate with males that are larger than themselves (Sato & Yoseda, 2010), increased fecundity may have nevertheless driven the evolution of a large body size in females and a pronounced male-biased SSD, though most likely in combination with other factors, such as predator avoidance and competition.

The last alternative explanation for the evolution of SSD proposes ecological causes, adapting the sexes to different ecological niches, e.g., regarding intersexual differences in diet and habitat (Shine, 1989). In species where growth continues after maturity, SSD may also reflect differences in survival (Shine, 1988). If male *B. latro* are more long-lived than females, they may be able to reach a larger body size than females. Even though the information on the longevity of *B. latro* in general, and that of females versus males in particular, is scarce, the few available studies do suggest that males are more long-lived (approx. 49 years) than females (approx. 33 years), that the age at which males reach 95% of the maximum asymptotic size in a growth curve is higher than that in females, and that individuals of *B. latro* generally have a comparatively long life span of 40 to 60 years (Fletcher et al., 1991a; Sato et al., 2013) (please, note, however, that these longevity estimates are based on body size!). Although adult *B. latro* have been reported to occur in a variety of habitat types and to consume a variety of different food items (Drew et al., 2010 and references therein), it has not been investigated whether there are general differences in habitat and dietary requirements between females and males. For gravid and ovigerous females on Christmas Island, the preferred habitats are reported to be humid, with ready access to fresh water, and a close vicinity to the ocean (Schiller et al., 1991). This may be due to the fact that: (i) vitellogenesis and egg incubation require access to water and inorganic ions (Schiller et al., 1991); (ii) egg maturation takes place outside the female body: the extruded egg mass is attached to the ventral surface of the abdomen by three biramous and setaceous pleopods, exposing the eggs to potential environmental threats (exposure to fresh and salt water, desiccation) (Reese & Kinzie, 1968; Reese, 1987; Hicks et al., 1990; Schiller et al., 1991; Sato & Yoseda, 2008); (iii) females hatch their eggs in the ocean (Greenaway, 2003). Additionally, the following reported differences in females and males may hint at and reflect different niches: (i) a great variation in sex ratios between populations on the same island (Rumpff, 1986, in Drew et al., 2010; Chauvet & Kadiri-Jan, 1999; personal observation); (ii) the more sedentary behaviour of females outside of the breeding season in comparison to males which more frequently exhibit non-migrational movements and are more gregarious (James, 2007); (iii) females migrate to the coast to spawn (Reese & Kinzie, 1968; Schiller et al., 1991), but there is no robust evidence for a female-only migration (Drew et al., 2010; Krieger et al., 2012; Sato & Yoseda, 2013); (iv) females are exposed to the force of waves during spawning (Reese & Kinzie, 1968; Schiller, 1993 in Drew et al., 2010); (v) females and males exhibit different growth increments at each moult (Fletcher et al., 1991a; Sato et al., 2013).

Shine (1989) pointed out that SSD may evolve in response to a combination of the different selective forces, instead of any one of these factors alone. This may of course also hold true for the SSD observed in *B. latro*.

Despite the evidence for the existence of SSD in *B. latro*, does the size of females and males in mating pairs reflect this SSD across the whole possible size range of sexually mature crabs? Females and males of *B. latro* are estimated to reach reproductive maturity at a TL of approx. 25 mm (Fletcher, 1993; Sato et al., 2008; Sato & Yoseda, 2008), but sexually mature females with TL <25 mm have been observed (Sato & Yoseda, 2008, 2010). In females, the presence of setae on the biramous pleopods distinguish sexually mature individuals from immature ones with non-setaceous pleopods, whereas in males, the presence of stable spermatophores (i.e., do not easily burst in contact with sea water) in the vasa deferentia has been used to define sexual maturity (Sato et al., 2008; Sato & Yoseda, 2008). Even though small males with a TL of approx. 25 mm may already carry stable spermatophores and thus be sexually mature, Sato et al. (2008) assume that they may not necessarily be sexually active and participate in mating, i.e., they may not be functionally mature, despite their investment in the production spermatophores. Within the possible size range of sexually mature crabs, males overlap with females at a TL of approx. 25–52 mm. However, do females preferably mate with males of a certain body size? Helfman (1973) suggested that female and male *B. latro* need to be of comparable sizes for successful mating. According to estimates of mating pairs in the field and mating trials in the laboratory carried out by Sato & Yoseda (2010), females prefer to mate with males that are larger or approximately equal to them in size. The authors covered a wide range of TLs: Estimates: 24.9–38.7 mm (females), 30.9–64.9 mm (males); mating trials: 28.7–37.5 mm (females), 25.0–58.5 mm (males). Additionally, when males in the mating trials had a TL which was approx. 2.5 mm larger than that of the female, fewer injuries or deaths occurred than in mating pairs where males were of the same size or smaller than females. Since sexually mature females with TL <25 mm have been observed (Sato & Yoseda, 2008, 2010) (potential reconsideration of the threshold limit value of 25 mm?), it is very likely that small males, if functionally mature, may only mate with females of a similar or even smaller size. On the other hand, large males above a TL of 52 mm (Amesbury, 1980) were assumed to be reproductively inactive, and were even suggested to compete with crabs of smaller reproductive size for food and potential burrowing sites (Helfman, 1973). Amesbury (1980), however, observed a high proportion of reproductively active females also in areas with the highest density of large males, and Sato & Yoseda (2010) and Sato et al. (2010) reported that in experiments carried out on *B. latro* from Hatoma Island, large males with a TL >52 mm were potent, provided larger numbers of sperm, and achieved higher fertilisation rates compared to smaller males. In addition, a study by Sato (2011) suggests that in wild populations, males with a TL >52 mm do participate in reproduction. Thus, the size assortative mating and the preference of females for larger males, together with the positive correlation between male body size and the number of spermatozoa, spermatophore volume, sperm passed to females, retained sperm reserves, and fertilisation rate in females (Sato et al., 2008, 2010; Sato, 2011), all indicate that the reproductive potential in male *B. latro* may be size-dependent.

Apart from a difference in body size and thus a pronounced SSD, the results in this study also indicate a pronounced sexual dimorphism in *B. latro* with regard to the size of the chelipeds. Even after size and shape correction, the size of male chelipeds was significantly larger than that of females, hence the greater cheliped size in males cannot solely be explained by the males' larger body size. Thus, there is a strong indication for the existence of selective forces related to the separate reproductive roles of female and male *B. latro*.

Static allometry. The allometric analyses of weight and several cheliped parameters in relation to thoracic length were carried out by applying and comparing a linear Model II regression and a Model II non-linear analog of Reduced Major Axis (RMA) regression. Regarding the state of allometry derived from the slope of the fitted equations for the analysed parameters, both methods yielded the same result. For some of the parameters, however, the values for the shape parameter as well as the allometric growth coefficient were very different, depending on the method of regression analysis applied. When comparing the graphics of the fitted models in the original bivariate data, the model fitted by the Model II non-linear analog of RMA regression mostly showed a better fit to the data than the model fitted by the linear Model II regression. This may speak for the use of non-linear regression analyses for future allometric studies.

The allometric equations calculated on the values of W in relation to TL indicate that the sampled individuals of *Birgus latro* grow isometrically, i.e., with no increase in relative thickness or plumpness with increasing body length. This is consistent with the state of allometry found by Amesbury (1980), who obtained a regression equation calculated on log-transformed data (allometric growth coefficient: 3.001). He was also able to include individuals with a much broader size range regarding TL (4–70 mm, compared to 36.6–72.5 mm in our study).

Unfortunately, there is no reference data on the allometric relationships for the measured cheliped parameters in relation to TL. Males as well as females may show different allometric relationships than the ones calculated in this study, with individuals of smaller TLs (males: TL <55.5 mm, females: TL <36.6 mm) being included. For the individuals of the sampled size range we may, however, conclude that the steeper allometric slopes in males compared to females hint at sexual selection as driving force for the allometry of male cheliped parameters, since sexually selected structures have often been shown to follow positive static allometry (Rosenberg, 2002; Kodric-Brown et al., 2006). This means that these structures show a faster growth rate in relation to a morphometric dimension of body size taken as a reference measure (Hartnoll, 1978, 1982, 1985). Until puberty moult, the growth of chelipeds in many decapod crustaceans is isometric, and continues to be so in sexually mature females, whereas in sexually mature males the level of allometry may increase (to positive allometry) and lead to an enlarged cheliped size relative to body size (Mariappan et al., 2000). However, structures following positive allometry may both be sexually as well as naturally selected (Bonduriansky, 2007; Bergmann & Berk, 2012). Irrespective of the selective force, the intersexual differences in allometric growth regarding the cheliped parameters most likely reflect the differences in cheliped size and heterochely between female and male *B. latro*.

Heterochely. The decapod cheliped is a multi-functional limb which may be used in foraging and food acquisition, agonistic interactions, and male-male competition for access to females (Lee, 1995). Different selection pressures as well as phylogenetic and developmental constraints may jointly determine the structure and size of chelipeds in decapod Crustacea. Similar to most hermit crabs of the families Diogenidae and Coenobitidae, female and male *Birgus latro* individuals have a directional asymmetry in size and shape between the left and right chelae ("handedness" or heterochely) (Palmer, 1996), with the dimensions of the left chela being larger than those of the right one (Fletcher, 1993; findings of this study). Asymmetry in hermit crabs is not restricted to the chelae, but is also expressed in the abdomen and abdominal appendages and is an adaptive response to the mostly asymmetric shape of the gastropod shell inhabited (Hazlett, 1981; Palmer, 1996; Møller & Swaddle, 1997): The outer face of the larger chela serves as a modified operculum for closing the shell aperture, and the abdomen conforms to the shell's spiral, with the asymmetric uropods grasping the columella (Blackstone, 1985). During different stages of its life cycle, the abdomen of *B. latro* undergoes a transition from symmetry (as zoeae) to asymmetry (as shell-inhabiting glaucothoë and early juvenile) and back to near-symmetry (as "free-living" later juvenile and adult, except for female pleopods) (Burggren & McMahon, 1988). However, the asymmetry of the chelae remains throughout adulthood in both sexes. Since *B. latro* has evolved from, and belongs to, shell-inhabiting left-handed hermit crabs, heterochely most likely reflects the retention of the ancestral body plan (Reese, 1968; Neville, 1976). Regarding the individuals investigated in our study, heterochely was significantly more pronounced in males compared to females, and in contrast to females, asymmetry could not only be observed in the propodus and dactylus, but also in the merus. In many hermit crab species, as well as many other anomuran and brachyuran species, heterochely is more pronounced in males than in females, presumably as a result of sexual selection. In many groups of Crustacea, weapons have evolved mainly in the form of enlarged, highly sexually dimorphic chelipeds (Emlen, 2008). In many heterochelous decapod crustaceans, the chelipeds of males are differentiated into a larger "crusher" and a minor "cutter" claw, based on morphological and functional aspects (Mariappan et al., 2000). In those cases, they evidently are used for specialised feeding, and heterochely may have evolved as a response. In other cases, e.g., fiddler crabs, males often use the major claw in contests over access to females, food or burrows, and females may assess from males' enlarged chelipeds the respective quality as a potential mate (Emlen, 2008). Intraspecific agonistic behaviour has repeatedly been observed in *B. latro* (see Helfman, 1973; Amesbury, 1980; personal observation), and may include the presenting of chelipeds (Drew et al., 2010). In agonistic encounters that may arise if the distance between these reportedly mostly solitary crabs (Fletcher, 1993) falls below a certain limit (one metre, as stated by Helfman, 1973), it is usually the individual with the smaller body size that succumbs and retreats (Helfman, 1973, 1977; Amesbury, 1980). However, it has not been investigated, which role the enlarged left cheliped (or generally, the larger male chelipeds compared to those of females) may play in these encounters, nor whether or to what extent it may act as a means for females to assess the quality of a male. The high level of aggressiveness reported for *B. latro* by some researchers (e.g., Helfman, 1977) may not always hold, at least not for all individuals. Especially with an abundant food source present, crabs may feed gregariously in greater numbers (Rumpff, 1986, in Drew et al., 2010), but they may also share burrows or sheltering/resting places, even in close physical contact (personal observation). So far it has not been reported which intrasexual behaviour males may exhibit in the presence of females and during reproductive activity.

Regarding feeding behaviour, the enlarged left cheliped in *B. latro* may play a role in accessing the pulp of the fruit of the coconut palm *Cocos nucifera*, which is rich in protein. *B. latro* usually feeds by using the enlarged cheliped for crushing and stripping and the smaller right cheliped for moving food particles to the maxillipeds (Burggren & McMahon, 1988). Crabs of large body size have been observed stripping coconuts off their outer husk (exocarp and mesocarp) using their chelipeds (Rumpff, 1986, in Drew et al., 2010), subsequently accessing the kernel by poking a hole through one of the "eyes" (germination pores) using the chelipeds or the pointed tips of their second pereiopods (Reese, 1987; Hicks et al., 1990). In view of the coconut's extremely hard shell as well as the strong chelipeds and climbing ability of *B. latro*, some naturalists and researchers have even pointed out a special association between the coconut and the coconut crab, assuming their coevolution (Harries, 1983). Thus, Parish (1910: 271) states: "These modifications, so extraordinary both in habits and in organs, and found in the *Birgus* alone, of all the crab family, could have been acquired by association with no other plant than the Coco Palm, and to account for their acquisition demands an immense period of time."

CONCLUSIONS

Our study confirms sexual dimorphism with regard to body size in sexually mature adult individuals of *Birgus latro*, and provides first statistical evidence for the existence of heterochely, as well as the existence of sexual dimorphism with regard to cheliped size and heterochely. In order to be able to better embed the findings into a broader evolutionary context, still more information on important facets of the life history of *B. latro* is needed. The information that is currently available indicates that sexual dimorphism with regard to body size has most likely evolved through sexual selection via female choice. There is yet a lack of evolutionary explanations for sexual dimorphism with regard to cheliped size and heterochely. Furthermore, the (adaptive) function of the enlarged left cheliped in both female and male individuals of *B. latro* is unknown.

In the near future, there may be a reduction especially in the average body size of males, due to selective harvesting of large males by humans on most islands still inhabited by *B. latro* (see Sato & Yoseda, 2010; Sato et al., 2010; Sato, 2012), with potentially dramatic consequences on the species' reproductive success. Additionally, introduced predators, such as the ant species *Anoplolepis gracilipes* on Christmas Island, may annihilate the advantage of the crabs' large body size evolved over millions of years. Addressing questions regarding reproductive potential, recruitment success, larval and juvenile ecology, as well as population structure and genetics of *B. latro*, will be essential in order to take adequate and immediate measures for its conservation and potential in vitro rearing. Despite the valuable information being rendered by thorough observational studies, there is a need for robust experimental research on *B. latro*. Due to the size and strength, as well as the slow growth of *B. latro*, this may not be an easy task, but would give invaluable insights into the life history of, and conservation measures for, this magnificent and majestic animal.

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