Article

Xylophagous millipede surface area to volume ratios are size-dependent in forests

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Abstract
A consistent effect of increasing precipitation (and resource abundance) on body size reductions is known as a water conservation hypothesis. Here a water conservation hypothesis was investigated in millipedes and a comparison made between high long-term mean annual precipitation of forest (750-1500 mm) and lower long-term mean annual precipitation of savanna (544 mm) biome species (n=29, 6). When the confounding effects of phylogeny, sexual dimorphism, sexual size dimorphism and size were controlled/removed, differences were found between six savanna species (*Bicoxidens brincki*, *Doratogonus annulipes*, *Harpagophora spirobolina*, *Julomorpha hilaris*, *J. panda*, *Odontopyge tabulinus*: 0,35975-2,632336 mm^{-1}) and 29 forest species (*Centrobolus*: 0,000113-0,679931 mm^{-1}; *Sphaerotherium*: 1,14271-3 mm^{-1}) in the surface area: volume ratios. Savanna millipedes had size-independent surface area: volume ratios (0,519783 mm^{-1} in males and 0,823878 mm^{-1} in females). Differences occurred between size-independent savanna and size-dependent forest taxa in surface area: volume ratios (t=3.75191, p=0.000013, n=58,12) controlling for the derivation whereby length/width increase affected surface area equally. Female savanna millipedes were longer than female forest millipedes (t=2.26165, p=0.016156, n=22, 6).

Keywords area; *Centrobolus*; conservation; *Sphaerotherium*; surface; volumes.

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1 Introduction

There was a consistent effect of increasing precipitation (and resource abundance) on body size reductions of an entire order of legless, predominantly underground‐dwelling amphibians (Gymnophiona, or caecilians), supporting the water conservation hypothesis (Lees, 1950; Pincheira-Donoso et al., 2019). The humidity (‘water conservation hypothesis’) “rests on three conditions: that spiracular transpiration is greater than cuticular transpiration; that cuticular transpiration rates are lower in desert species; and that changes in body form associated with flightlessness lead to an overall reduction in water loss rates. The extreme form of the morphological-convergence condition suggests that this change in body shape should be most pronounced in desert-dwelling taxa" such as beetles (Chown et al., 2011).

Here the water conservation hypothesis was investigated in millipedes. Smaller millipedes, having lower water reserve, higher cuticular permeability values and a higher rate of per cent of total body water loss, were found to be less tolerant to desiccation compared with larger species (Bhakat, 2014). Water relations in the desert millipede *Orthoporus ornatus* is considerably greater than in millipedes previously studied (Crawford, 1972). The percentage of total body water loss increases linearly with desiccation time in the garden millipede *Oxidus gracilis* (Appel, 1988). Water is readily lost and taken up through the cuticle, the effect of the spiracles and of excretion being negligible (Cloudsley-Thompson, 1950). It was also noted the percentage water content of smaller millipedes is greater than larger ones (Baker, 1980).

Here a comparison was made between millipede species of forest and savanna biomes (Geldenhuys, 1989; Kulmatiski and Beard, 2013). When the confounding effects of sexual size dimorphism were removed, differences were investigated between species of the savanna species and their forest counterparts in surface area to volume ratios.

2 Materials and Methods

2.1 Morphometrics calculations

Body volumes, surface areas and surface area to volume ratios were calculated in 28 forest species compared to 6 savanna species. Two morphometric parameters were used to obtain measurements, length and width, both of which were obtained from the published literature (Cooper, 2018; Cooper, 2019; Lawrence, 1967; Schubart, 1966) (Table 1). Body volumes were calculated based on the formula for a cylinder $V = \pi r^2 h$ and surface areas were calculated based on the formula for the same cylinder $SA = 2\pi r(r+h)$ in all species except *Sphaerotherium* pill millipedes where the body volume formula was $V = 4\pi r^3/3$ and surface area was $SA = 4\pi r^2$.

2.2 Statistical tests

Body volumes, surface areas and surface area to volume ratios of male and female millipedes for the 28 forest and 6 savanna species were tabulated using a Microsoft Excel spreadsheet. The One-Way ANOVA was performed using summary data to test for differences between taxa using a Free Statistics Calculator version 4.0 available at https://www.danielsoper.com/statcalc/calculator.aspx?id=43. Values were then compared using the http://www.socscistatistics.com website *t*-test for 2 independent means. Males and females were compared with respect to body volumes, surface areas and surface area to volume ratios across the forest and savanna biomes. Then males were added to females and forest genera (Table 2) compared to each other and to savanna taxa which were pooled (Table 3).

2.3 Control

I controlled for the confounding effects of phylogeny, sexual dimorphism, sexual size dimorphism and size in each comparison.

2.4 Environmental variables

The long-term mean annual precipitation in the savanna was recorded at 544 mm (Kulmatiski and Beard, 2013), and in the forest was estimated at 750-1500 mm (Geldenhuys, 1989).

3 Results

3.1 Linear measurements

Savanna millipedes differed in length compared to forest millipedes (ANOVA: F=2.897, d.f.=3, P=0.042). Savanna millipedes differed in width compared to forest millipedes (ANOVA: F=16.200, d.f.=3, P=0.000).

Female savanna helminthomorph millipedes differed from female forest helminthomorph millipedes in length (t=-2.35263, p=0.013091, n=22, 6) but not width (t=1.67428, p=0.053032, n=22, 6). Male savanna helminthomorph millipedes did not differ from male forest helminthomorph millipedes in length (t=-1.40834, p=0.085673, n=22, 6) or width (t=0.79823, p=0.215983, n=22, 6). Female savanna millipedes did not differ from female forest millipedes in width (t=1.61841, p=0.057547, n= 29, 6). Female savanna millipedes were different from female forest millipedes in length (t=-2.26165, p=0.016156, n=22, 6).

3.2 Volumes

Forest taxa were indifferent to savanna taxa in volume (t=-1.18061, p=0.120627, n=58, 12; ANOVA: F=2.586, d.f.=3, P=0.060). *Centrobolus* males differed from females in volume (t=2.19256, p=0.016965, n=22, 22). *Sphaerotherium* males were marginally different from females in volume (t=-1.76762, p=0.05126, n= 7, 7). *Centrobolus* males differed from *Sphaerotherium* males in volume (t=4.15584, p=0.000146, n=22, 7). *Centrobolus* females did not differ from *Sphaerotherium* females in volume (t=2.52508, p=0.008874, n=22, 7). A combination of the forest taxa *i. e. Centrobolus* and *Sphaerotherium* differed between sexes (ANOVA: F=5.081, d.f.=1, P=0.028). Forest males were no different to savanna males (t=0.26026, p=0.398016, n=35, 6) while forest females were not different to savanna females (t=-1.28835, p=0.102608, n=35, 6).

3.3 Surface areas

A difference was present among forest and savanna millipede surface areas (ANOVA: F=341,864.807, d.f.=3, P=0.000). *Centrobolus* males did not differ from females in surface area (t=-1.24616, p=0.108044, n=22, 22). *Sphaerotherium* males were marginally different from females in surface area (t=-1.75744, p=0.5215, n=7, 7). Forest taxa did not differ from savanna taxa in surface area (t=-0.32209, p=0.374262, n=58, 12). When sexual size dimorphism was controlled (and *Sphaerotherium* excluded) in a comparison between *Centrobolus* and savanna taxa no difference was found in the surface areas (t=0.45811, p=0.32389, n=44, 12).

3.4 Surface area to volume ratios

When the forest data set was compared with the savanna (males and females added) a significant difference was found in surface area to volume ratios (t=-3.75191, p= 0.000013, n=58, 12; ANOVA: F=12,927,853.340, d.f.=3, p=0.000). Male and female *Centrobolus* surface area to volume ratios were not significantly different (t=0.44722, p=0.327921, p<0.10, n=22, 22). The same was true for *Sphaerotherium* male and female surface area to volume ratios which were indifferent (t=-0.32315, p=0.749501, p<0.10, n=7, 7). Because of this, differences were investigated between species belonging to forest and savanna biomes and there were no differences between male savanna millipede surface area to volume ratios and male forest millipede surface area to volume ratios (t=-2.44161, p=0.008655, n=28, 6). There was a significant difference between forest millipede female surface area to volume ratios and savanna millipede female surface area to volume ratio (t=-2.83273, p=0.003045, n=28, 6) but there was no difference between male and female savanna millipede surface area to volume ratios (t=-0.47794, p=0.637407, n=6, 6). When I controlled for phylogeny differences occurred between the surface area to volume ratios of female forest *Centrobolus* and female (t=-3.39958, p=0.000638, n=22, 6) and male (t=-2.43107, p=0.009202, n=22, 6) savanna millipedes but not with the *Sphaerotherium* males (t=-1.77194, p=0.041023, n=22, 6) or females (t=-2.23741, p=0.014665, n=22, 7). Male forest *Centrobolus* differed from female savanna millipedes (t=3.96105, p=0.00011, n=22, 6) and male savanna millipedes (t=-2.88846, p=0.00278, n=22, 6) in surface areas. When sexual size dimorphism was controlled and the sexes were added, there was a difference between the surface area to volume ratios of *Centrobolus* and *Sphaerotherium* (t=-3.22188, p=0.000836, n=44, 14).

. **Table 1** Male and female morphometric parameters recorded in savanna and forest millipedes.

Species	**Male length (mm)**	**Male width (mm)**	**Female length (mm)**	**Female width (mm)**
B. brincki	93	5.9	84	5.9
C. albitarsus	39	4.0	50	6.0
C. anulatus	69	5.3	76	5.9
C. decoratus	43	4.5	31	4.2
C. digrammus	41	4.0	34	4.4
C. dubius	52	5.0	51	5.9
C. fulgidus	54	5.2	52	6.8
C. immaculatus	49	4.7	60	7.0
C. inscriptus	67	5.9	63	6.7
C. inyanganus	40	4.5	43	5.2
C. lawrencei	43	4.7	43	5.9
C. lugubris	53	6.2	63	8.4
C. promontorius	33	3.6	27	3.3
C. pusillus	39	4.0	40	5.7
C. richardi	59	5.2	50	5.5
C. ruber	58	5.0	62	6.1
C. rugulosus	49	5.4	50	7.5
C. sagatinus	49	6.2	48	7.0
C. silvanus	46	4.4	44	4.8
C. titanophilus	28	4.1	29	4.3
C. transvaalicus	39	4.4	38	5.0
C. tricolor	45	4.5	37	5.2
C. vastus	65	6.0	63	8.2
D. annulipes	104	5.5	89	5.9
H. spirobolina	72	4.4	79	5.9
J. hilaris	26	2.4	28	3.7
J. panda	32	4	38	2.7
O. tabulinus	63	5	70	5
S.cinctellum		15.5		18.6
S. commune		6		9.5
S. punctulatum		12		21
S. spinatum		11.5		15
S. tenuitarse		7		8
S. trichopygum		10.75		16.5
S. tuberosum		6.75		9

Table 2 Surface area to volume ratios for forest millipedes (*Centrobolus, Sphaerotherium*).

Species	**Male volume (mm^3)**	**Female volume (mm^3)**	**Male surface area (mm^2)**	**Female surface area (mm^2)**	**Male surface area: volume (mm^{-1})**	**Female surface area: volume (mm^{-1})**
C. albitarsus	1960	5655	1 080,708	2 111,15	0,00051	0,000177
C. annulatus	2058	1729	2462,874	3026,009	0,000486	0,000578
C. decoratus	2736	1718	1 343,031	928,906	0,000365	0,54069
C. digrammus	2061	2068	1 130,973	1 061,607	0,000485	0,000484
C. dubius	4084	5577	1 790,708	2 109,328	0,000245	0,000179
C. fulgidus	4587	7554	1 934,216	2 512,269	0,000218	0,000132
C. immaculatus	3400	9236	1 585,813	2 946,814	0,000294	0,000108
C. inscriptus	7327	8885	2 717,289	2 934,185	0,000136	0,000113
C. inyanganus	2545	3653	1 258,208	1 574,818	0,000393	0,000274
C. lawrencei	2984	4702	1 408,627	1 812,762	0,000335	0,000213
C. lugubris	6400	13965	2 306,18	3 768,403	0,000156	0,000716
C. promontories	1343	924	827,872	628,256	0,616435	0,679931
C. pusillus	1960	4083	1 080,708	1 636,707	0,00051	0,000245
C. richardi	5012	4752	2 098,579	1 917,942	0,418711	0,403607
C. ruber	4555	7248	1 972,92	2 621,596	0,00022	0,000138
C. rugulosus	4489	8836	1 845,749	2 709,624	0,000223	0,000113
C. sagatinus	5913	7389	2 150,357	2 419,026	0,000169	0,000135
C. silvanus	2798	3185	1 393,359	1 471,773	0,000357	0,000314
C. titanophilus	1479	1685	826,93	899,689	0,559114	0,53394
C. transvaalicus	2372	2985	1 199,837	1 350,885	0,000422	0,000335
C. tricolor	2863	3143	1 399,58	1 378,782	0,000349	0,000318
C. vastus	7351	13308	2 676,637	3 668,375	0,000136	0,000751
S. cinctellum	1950	3369	3 019,071	4 347,462	1,548205	1,290294
S. commune	113	449	452,389	1 134,115	4	2,525612
S. punctulatum	905	4849	1 809,557	5 541,769	2	1, 14271
S. spinatum	796	1767	1 661,903	2 827,433	2,08794	1,599887
S. tenuitarse	180	268	615,752	804,248	3,422222	3
S. trichopygum	650	2352	1 452,201	3 421,194	2,233846	1,454507
S. tuberosum	161	381	530,929	1 017,876	3,298137	2,671916

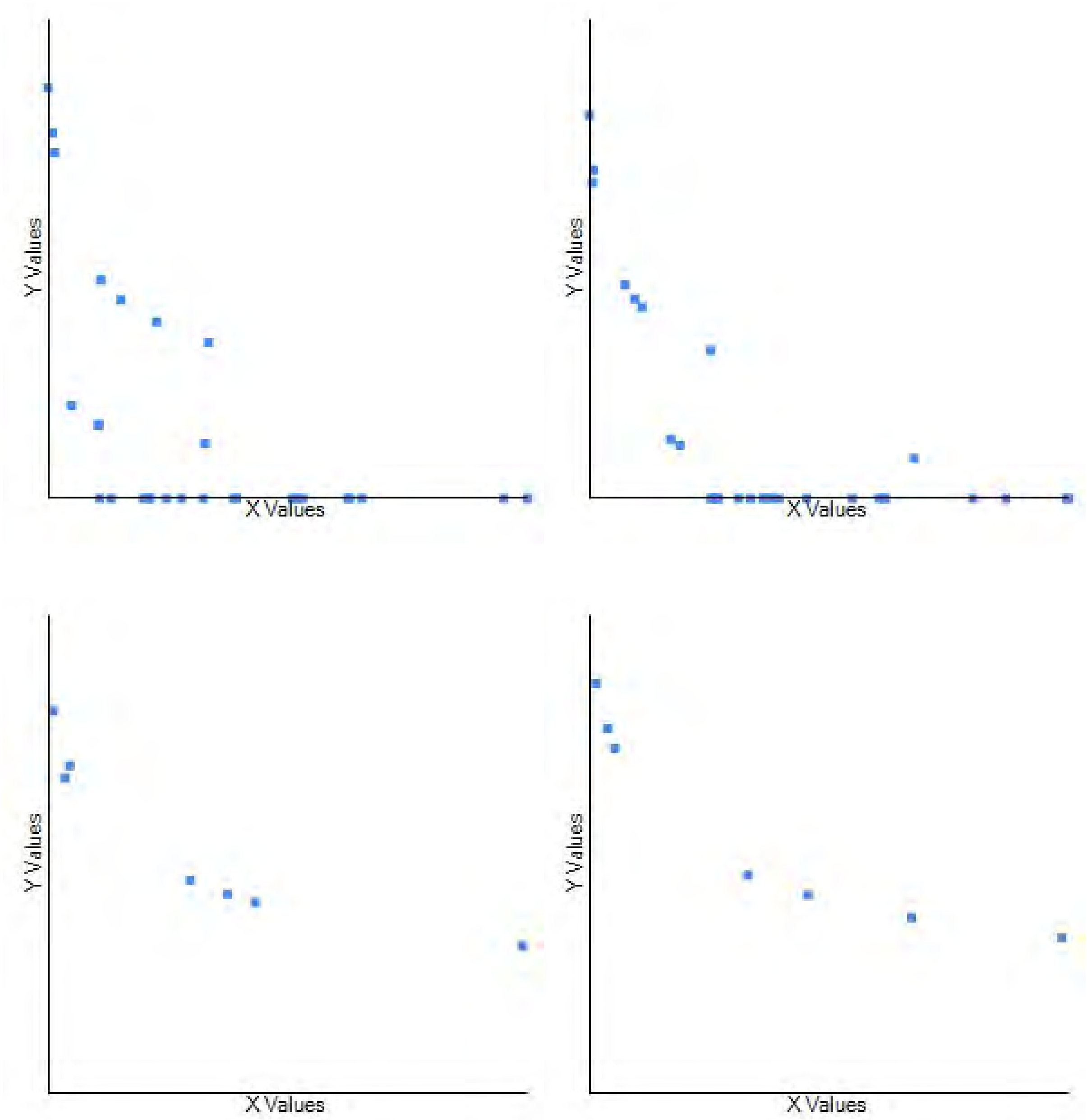

Fig. 1 Size-dependent relationships between the surface area to volume ratios and volume in female forest millipedes (top-left), male forest millipedes (top-right), female *Sphaerotherium* (lower-left) and male *Sphaerotherium* (lower-right). All X-values are volume and Y-values are surface area to volume ratios.

Surface area to volume ratio was negatively correlated with volume in female *Centrobolus* (r=0.4577, r^2=0.2095, n=22, p=0.032499), female *Sphaerotherium* (r=0.9118, r^2=0.8314, n=7, p=0.004324), and female forest millipedes in general (r=-0.5542, r^2=0.3071, n=29, p=0.00182). This correlation was not found in male *Centrobolus* (r=-0.2836, r^2=0.0804, n=22, p=0.20189), but was found in male *Sphaerotherium* (r=-0.8728, r^2=0.7618, n=7, p=0.010496) and was found in forest male millipedes in general (r=-0.6529, r^2=0.4263, n=29, p=0.000123). Surface area to volume ratios did not correlate with volume in savanna males (r=-0.1538, r^2=0.0237, n=6, p=0.770826) or females (r=-0.2131, r^2=0.0454, n=6, p=0.685332).

Table 3 Surface area to volume ratios of savanna millipedes (*Bicoxidens*, *Doratogonus*, *Harpagophora, Julomorpha, Orthoporoides*).

Species	**Body volume (mm^3)**		**Surface area (mm^2)**		**Surface area: Volume (mm^{-1})**	
	Male	Female	Male	Female	Male	Female
B. brincki	10 300,656	9 275,598	3 695,762	3 345,919	0,358789	0,360723
D. annulipes	9 899,293	9 858,974	3 789,809	3 546,761	0,382836	0,35975
H. spirobolina	4 391,946	8 639,348	2 111,37	3 147,31	0,480737	0,364299
J. hilaris	474,104	1 195,634	431,278	3 147,31	0,90967	2,632336
J. panda	1 608,495	865,704	904,779	687,066	0,5625	0,79365
O. tabulinus	5 170,96	5 407,625	2 193,341	2 338,853	0,424165	0,43251

4 Discussion

Millipede species-specific volumes are known to exist and these correlate with bimaturism, copulation duration, fecundity, female body width, sexual conflict, sexual size dimorphism, species and mass (Cooper, 2016-2019). Forest millipede surface area to volume ratio was size-dependent (Fig. 1) while in savanna millipedes it was size-independent. The significant difference between forest millipede female surface area to volume ratios and savanna millipede female surface area to volume ratio was a finding which suggests differences in the form in agreement with the water conservation hypothesis (Lees, 1950). It suggests there are precipitation-size patterns in worm-like millipedes which may affect the adaptability to and validity of biological rules (Meiri and Dayan, 2003; Schmidt-Nielson, 1984). Although sexual dimorphism is not clearly evident in the savanna biome their size is thought to be mostly longer (Cooper, 2019). Where there is the confounding effect of sexual dimorphism in the forest millipedes there was a relationship between the surface area to volume ratios and volume. When the effect of sexual dimorphism was removed and surface area to volume ratios were compared, savanna and forest taxa showed a significantly different surface area to volume ratio. Surface area to volume ratios was higher in the savanna taxa although forest taxa were also high due to *Sphaerotherium*. How do millipedes maximize their size – through an increase in width or length of their cylindrical bodies? It was achieved through a change in width and length, which is probably the most powerful way to maximize the volume and surface area to volume ratio of a cylinder, which is anamorphosis (Enghoff, 1993).

A further difference within forest millipede surface area to volume ratios between the genera *Centrobolus* and *Sphaerotherium* indicate divisions within the forest taxa suggesting there is water conservation stress within the forest as well. The forest genus *Sphaerotherium* illustrated the most differences with volume, surface area and surface area to volume ratios all being different and a strong relationship between volumes and surface area to volume ratios. This genus is related to *Glomeris* and the water relations were attributed to size and conglobation (Edney, 1951). Conglobation in the pill bug (*Armadillidium vulgare*) is an adaptive water conservation mechanism (Smigel and Gibbs, 2008). When phylogeny, sexual size dimorphism, and sexual dimorphism were controlled a difference was found in the surface area to volume ratios between the forest and savanna sample but not volumes. This was evident in the presence of a relationship between forest surface area to volume ratios and volume which was absent in the savanna taxa. It proves forest millipedes which cannot conglobate also conserve water adaptively through the surface area to volume ratios dependent on size. Smaller juliform millipedes, having lower water reserve, higher cuticular permeability values and higher rate of percent of total body water lost, are known to be less tolerant to desiccation compared with larger species (Bhakat, 2014). Therefore the size-dependent surface area to volume ratios of forest millipedes is predictably less tolerant to desiccation while the size-independent surface area to volume ratios of savanna millipedes are predictably intolerant to desiccation. Water relations in the desert millipede *Orthoporus ornatus* is considerably greater than in millipedes previously studied (Crawford, 1972). The percentage of total body water loss increases linearly with desiccation time in the garden millipede *Oxidus gracilis* (Appel, 1988). Water is readily lost and taken up through the cuticle, the effect of the spiracles and of excretion being negligible (Cloudsley-Thompson, 1950). It was also noted the percentage water content of smaller millipedes is greater than larger ones (Baker, 1980). Energy and water balances vary from tropical to desert biomes and can also change temporally which are behaviourally modified and independent of surface area to volume ratios but dependent on genera (Clousley-Thompson, 1959; Crawford, 1978; Webb and Telford, 1995). In order to conserve water, the terrestrial arthropods have also acquired a relatively impervious integument (Dwarakanath and Job, 1965).

The significantly higher surface area to volume ratios of female forest millipedes compared to female savanna millipedes suggests a combined effect of fecundity selection together with water conservation. This is seen and probably thought to be caused due to a difference in lengths of the two, which affects the surface area of the cylindrical body form as powerfully as width which was the case. The savanna millipedes had longer females than the shorter forest female millipedes. This suggests millipede body size can change independent to temperature especially in the size-independent savanna millipedes (Enghoff, 1992; Golovatch and Kime, 2009). Behavioural differentiation and different use of time budget may contribute to the trophic niche separation among coexisting millipede species and in this instance sexes because distance passed per day correlates with body length (Semenyuk and Tiunov, 2019). Surface area to volume ratios is affected more through changes in width than length which is seen in the female differences due to fecundity selection (Darwin, 1874).

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