HERITABILITY OF MUSCLE SIZE IN EASTERN KINGBIRDS[1]

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Abstract. Heritability of the size of a hindlimb muscle, M. flexor cruris lateralis (FCRL), was analyzed in Eastern Kingbirds (*Tyrannus tyrannus*) to assess the potential of the trait to be influenced by evolutionary processes. Size of the FCRL appears to be highly heritable, although the birds are directionally asymmetrical and this asymmetry suggests that muscle size probably is not presently under rigid selective control. Heritabilities were recalculated after the removal of cases of doubtful parentage; the results lend support to a hypothesis of "quasi nest-parasitism" for Eastern Kingbirds.

Key words: Tyrannus tyrannus; *heritability; muscle size; asymmetry; nest parasitism; selection.*

INTRODUCTION

Heritability estimates have been used to test the potential of a phenotypic trait to respond to natural or artificial selection (Falconer 1981, Boag and Van Noordwijk 1987). They may also provide clues about the historical significance of differences among populations; if such differences have a genetic origin they may flag evolutionary units that can form the basis for questions about phylogenetic relationships, biogeography, evolution of morphology, and the origin of adaptive patterns (James 1983, McKitrick and Zink 1988). Traits investigated in birds to date have included body weight (Boag and Grant 1978; Smith and Zach 1979; Van Noordwijk et al. 1980, 1988; Garnett 1981; Grant 1981, 1983; Lessells 1982; Moss and Watson 1982; Boag 1983; Schluter and Smith 1986), hatching weight (Moss and Watson 1982), clutch size (Perrins and Jones 1974; Van Noordwijk et al. 1980, 1981a; Findlay and Cooke 1983; Gibbs 1988), egg dimensions (Ojanen et al. 1979; Van Noordwijk et al. 1980, 1981c; Moss and Watson 1982), wing length (Brooke 1977; Boag and Grant 1978; Smith and Zach 1979; Garnett 1981; Grant 1981, 1983; Boag 1983; Schluter and Smith 1986), tarsus length (Brooke 1977; Boag and Grant 1978; Smith and Zach 1979; Smith and Dhondt 1980; Garnett 1981; Grant 1981, 1983; Dhondt 1982; Lessells 1982; Boag 1983; Alatalo et al. 1984; Alatalo and Lundberg 1986; Schluter and Smith 1986; Van Noordwijk et al. 1988), beak dimensions (Brooke 1977; Boag and Grant 1978; Smith and Zach

1979; Smith and Dhondt 1980; Grant 1981, 1983; Lessells 1982; Boag 1983; Schluter and Smith 1986), laying date (Van Noordwijk et al. 1980, 1981b), hatching date (Findlay and Cooke 1982), dispersal distance (Greenwood et al. 1979, but see Van Noordwijk 1984), and viability (Moss and Watson 1982). Using primarily linear regression of offspring on parents and/or intraclass correlations of siblings (Falconer 1960, 1981), these studies have shown many of these traits to have fairly high, significant additive genetic variance.

In an earlier study (McKitrick 1985, 1986), I found extensive individual variation in an internal morphological trait: size of a hindlimb flexor muscle (M. flexor cruris lateralis: FCRL); numerous species of kingbirds (Tyranninae) show such intraspecific variation. This variation exhibits a trend towards reduction of the accessory portion of the muscle, as determined by outgroup comparison (McKitrick 1985, 1986). The muscle flexes the shank (crus) and is important in walking movements. Most kingbirds, particularly members of the genus *Tyrannus*, appear to use their hindlimbs for little besides perching. Typically these birds forage in a stationary fashion by perching for long periods while scanning their surroundings for aerial insects; they may also "hover-glean" insects from the surface of vegetation (Fitzpatrick 1980, 1981). Foraging on the ground is rare. Thus the muscle appears to be relatively unimportant in the daily activities of kingbirds.

Numerous examples of the evolutionary loss of useless structures exist, although the mechanisms and explanation for such loss remains speculative (see Regal 1977). The variation in M. flexor cruris lateralis may represent a stage

in the loss of that muscle. The present study is an attempt to test whether the variation in FCRL is heritable in Eastern Kingbirds (*Tyrannus tyrannus*), and thereby to discover whether or not such variation can be influenced by evolutionary processes, such as natural selection in the direction of eventual loss of the muscle.

METHODS

Twenty-eight families of Eastern Kingbirds (*Tyrannus tyrannus*) comprising 134 individuals were collected in northern lower Michigan during June through August 1985, 1986, and 1987 (22, 3, and 3 families, respectively). Nests were located by observing the behavior of the highly territorial adults. Adults were identified as being associated with a nest by their behavior, usually in that they fed the young in that nest and behaved territorially in the vicinity of the nest. If more than two adults were present, no birds were collected at that nest. Parents were collected with a .410 shotgun and nestlings were subsequently removed from the nest (except Family 2, see below). Of these 28, both parents were collected for 21 families and one parent was obtained for the remainder. For behavioral reasons it was thought that the adults in Family 2 might not have been the parents of the single, fledged offspring in that group; this group was eventually omitted from analyses.

Each family contained between one and four offspring. Fresh heart, liver, and muscle tissue from each specimen were preserved in liquid nitrogen and later transferred to a freezer at $-70°C$ for later analysis (see McKitrick 1990). The birds were then fixed in 10% formalin solution and preserved in 70% ethanol.

Variation in FCRL was measured as the length of the insertion of pars accessoria on the femur, from the proximal end of the semitendinous insertion to the medial epicondyle of the femur (see illustrations in McKitrick 1985, 1986). Measurements were taken of muscle insertion and femur length on the left and right sides, using a Fowler Ultra Cal II needle-nose digital caliper. Birds were measured at random rather than by family group. Because offspring were usually smaller than their parents and of varying age and size (see Appendix for ages), insertion length was initially divided by femur length to standardize measurements. Analyses were performed on untransformed data as well as on ratios. Measurement error was estimated for each side by measuring 10 adults and 10 juveniles once each on each of four consecutive days and calculating repeatability using analysis of variance (Sokal and Rohlf 1969, Falconer 1981, Boag 1983, Lessells and Boag 1987).

Heritability (h^2) was estimated in four ways: (1) full-sibling correlation using univariate one-way ANOVA; (2) linear regression using midparent-average offspring values; (3) single-parent-average offspring regression; (4) midparent, father, and mother-single-offspring regression (Falconer 1981). Sexes were pooled for calculation of average offspring values in each family.

To ensure that significant results were not obtained by chance, a form of data "cross-fostering" or bootstrapping was employed, whereby the parental measurements were shifted among offspring. The data set used for the original mother-single offspring regression was replicated 3,000 times using the Michigan Interactive Data Analysis System, and each of the 24 mothers was randomly assigned, without replacement, to one of the 72 offspring. Regressions were then calculated for left and right sides for each of these 3,000 data sets.

McKitrick (1990) demonstrated the occurrence of multiple parentage in this sample of kingbirds. Heritabilities based on single parent-single offspring regression were therefore recalculated with omission of (1) families with a definite paternal exclusion and those with an exclusion of either parent (for male-offspring regressions); (2) families with a definite maternal exclusion and those with an exclusion of either parent (for female-offspring regressions); (3) only families with a definite paternal exclusion (male parent-offspring regressions); (4) only families with a definite maternal exclusion (female parent-offspring regressions). Furthermore, Family 2 was excluded for the reasons stated above, and Family 1 was excluded due to poor electrophoretic resolution. The results are shown in Table 7 (see also McKitrick 1990; Appendix I).

RESULTS

MEASUREMENT ERROR

Measurement repeatability over the 4-day test period was high, averaging 0.95 for insertion length and 0.98 for femur length (Table 1). Error was somewhat higher for offspring insertion length than for adults; the muscles of the youngest offspring were more poorly defined, making

TABLE 1.   Repeatabilities of measurements of 10 adult and 10 nestling *Tyrannus tyrannus* measured over a 4-day period.

	Adults		Nestlings	
	Left	Right	Left	Right
Insertion length	0.95	0.98	0.90	0.88
Femur length	0.97	0.98	0.99	0.99

TABLE 3.   Correlation coefficients for between-mate comparisons ($n = 19$).

	Left	Right
Insertion length	0.04	0.02
Femur length	0.12	−0.06
Insertion/femur length	0.05	0.07

it difficult to take accurate measurements. Measurement error was similar on left and right sides.

ONTOGENY OF M. FLEXOR CRURIS LATERALIS

Nothing is known about the prehatching development of M. flexor cruris lateralis in kingbirds. However it is important to note that variation manifested in the adult morphology is also present in nestlings, and the variance is almost as great (see Table 2). Because use (=nonuse) of the muscle is equal among nestlings, this factor does not explain differential development of the muscle among offspring.

ASSORTATIVE MATING

Correlation between mates can have a significant effect on estimates of heritability (Boag and Grant 1978, Boag 1983, Hailman 1986). In Eastern Kingbirds, there was no significant correlation between mates for insertion length, femur length, or the ratio of insertion/femur length (Table 3).

ASYMMETRY

Juveniles and adults showed significant directional asymmetry, with a bias toward larger muscle insertion size on the right (pairwise *t*-test, juveniles: $t = -2.21$, $P = 0.03$; adults: $t = -2.04$, $P = 0.05$). There was no significant sexual dimorphism for insertion length (pairwise *t*-test, left side: $t = -0.58$, $P = 0.57$; right side: $t =$

-0.02, $P = 0.99$), and the sexes were pooled for this analysis.

RELATIONSHIP OF INSERTION LENGTH TO BODY SIZE

The length of insertion of FCRL was not correlated with femur length or body weight in adults or juveniles (see Table 4). Mean and variance of insertion length were uncorrelated within groups of siblings (left side: $r = 0.15$; right side: $r = 0.04$). The similarity in results of analyses using ratios and untransformed insertion length (see below) also point to a lack of relationship between body size and insertion length. Table 4 indicates a significant correlation between femur length and body weight in juveniles, but not in adults. However, this is probably due to the larger weight range represented in the juvenile sample compared with the adult sample (adult range = 38–42 g, juvenile range = 17–40 g). When the correlation analysis is limited to juveniles in the 35 to 40 g range, this relationship disappears ($r = -0.03$ for the left side, $r = 0.13$ for the right side).

HERITABILITY

Inspection of histograms indicated that the data were not normally distributed, whether in the form of untransformed insertion lengths or ratios. A normal distribution was not achieved by log, arcsin, or square-root transformations. It is probable that a larger sample is needed to de-

TABLE 2.   Descriptive statistics for left and right insertion lengths in adults and nestlings.

Variable	n	Minimum	Maximum	$\bar{x}$	SD
Adults					
Left insertion length (mm)	46	0.39000	3.5900	1.8561	0.67316
Right insertion length (mm)	44	0.46000	4.3800	1.9709	0.70302
Nestlings					
Left insertion length (mm)	78	0.76000	3.2000	1.8897	0.58295
Right insertion length (mm)	79	0.10000	3.8100	1.9847	1.1362

TABLE 4.   Correlation of insertion length with femur length and body weight.

Adults ($n = 39$)				
femleft	0.1616			
insrt	0.8144	0.0480		
femrt	0.1377	0.9604	0.0702	
weight	−0.0120	0.2341	0.0216	0.1675
	insleft	femleft	insrt	femrt
Juveniles ($n = 60$)				
femleft	−0.1346			
insrt	0.7743	−0.1160		
femrt	−0.0914	0.9810	−0.1069	
weight	−0.1327	0.8548	−0.0914	0.8259
	insleft	femleft	insrt	femrt

termine whether the data are truly nonnormally distributed.

The results of analyses using the ratio of insertion length to femur length were very similar to those using insertion length alone; there is no significant relationship between insertion length and femur length or body weight (Table 4), therefore only the results of the analyses using the untransformed data are presented.

Full-sibling correlation. Heritability estimates using the intraclass correlation were highly significant based on ratios and on untransformed insertion lengths for both left and right sides (Table 5).

Regressions. All regression analyses (Table 6) show a difference in significance of heritability estimates for the left and right sides, as well as differences in h^2 estimates based on male and female parents; muscle size generally has more highly significant heritability for female-offspring regressions and for the left side of the bird. On the left side, heritability estimates for average-offspring regressions ranged from 0.65 to 0.83 ($P = 0.002$ to 0.08), with the male-parent analysis being nonsignificant; when the Family 13 outlier was excluded from the female parent analysis, h^2 dropped from 0.74 to 0.59 ($P = 0.02$).

On the right side, for average-offspring analyses, heritability was significant only for esti-

mates based on female parent-offspring regressions and only when the outlier was included ($h^2 = 0.64$, $P = 0.02$).

For single offspring regressions, h^2 was significant (h^2 ranged from 0.48 to 0.72, $P = 0.0000$ to 0.04) in all analyses except right side, male parent. Exclusion of the Family 13 outlier did not change the results drastically.

"Cross-fostering" the data indicates that these results are highly unlikely to be obtained by chance. Of the 3,000 regression coefficients obtained for the left side (range = −0.31 to 0.33, $\bar{x} = 0.0006$, SD = 0.096), 100% fell below the minimum coefficient of 0.33 for true mother-single offspring regressions (see Table 6). For the right side 99.9% of the 3,000 coefficients (range = −0.37 to 0.34, $\bar{x} = -0.0017$, SD = 0.10) fell below the minimum coefficient of 0.29 for true mother-single offspring regressions.

For the recalculations of heritability after removal of cases of doubtful parentage, female parent-offspring regressions yielded higher h^2 in all cases for the left side of the bird, with significance remaining very high (Table 7). For the right side, h^2 increased only when definite maternal exclusions were removed from the analysis; h^2 dropped when definite maternity exclusions plus ambiguous parental exclusions were omitted. Omitting ambiguous parental exclusions and/or definite

TABLE 5.   Heritability estimates based on full-sibling correlation (univariate one-way ANOVA) using untransformed insertion length.

	Left				Right		
h^2	r	P	n	h^2	r	P	n
0.77	0.386	0.0006	74	0.70	0.35	0.001	75

TABLE 6.   Heritability estimates based on regressions using muscle insertion length.

	Left					Right				
	h²	SE	r²	P	n	h²	SE	r²	P	n
Midparent—average offspring	0.65	0.18	0.45	0.002	19	0.35	0.48	0.12	0.17	17
Male parent—average offspring	0.83	0.45	0.15	0.08	22	0.25	0.42	0.02	0.56	22
Female parent—average offspring	0.74	0.20	0.39	0.002	23	0.64	0.25	0.24	0.02	22
	(0.59	0.20	0.28	0.02	22	0.38	0.31	0.07	0.24)*	21
Midparent—single offspring	0.71	0.15	0.29	0.0000	57	0.48	0.16	0.15	0.005	51
Male parent—single offspring	0.69	0.33	0.06	0.04	69	0.42	0.30	0.03	0.2	67
Female parent—single offspring	0.72	0.17	0.23	0.0001	66	0.67	0.18	0.18	0.0005	64
	(0.66	0.17	0.19	0.0003	65	0.59	0.2	0.13	0.005)*	63

* With outlier (Family 13) excluded.

paternal exclusions resulted in nonsignificant heritabilities in all cases on both left and right sides in males.

DISCUSSION

Heritability estimates using full-sibling correlations (Table 5) and midparent-single offspring or single parent-single offspring regressions (Table 6) appear to be the most appropriate for this data set, because they tend to swamp the effects of outliers. Except for the male parent-single offspring regression of measurements of the right leg, these analyses yielded significant or highly significant heritabilities, ranging from 0.48 to 0.77. Midparent or single parent-average offspring analyses gave comparable h² values and significant results for the left side, but not for the right side (unless the outlier was included in the female-average offspring regression) and not for males. These estimates are within the range of values obtained for external morphological traits in other populations of wild birds (see references above).

The differences in significance of heritability estimates obtained using female parent and male parent-average offspring may be negligible, given the small sample size and the magnitude of the standard errors (see Table 6). If these differences are meaningful, however, they raise the possibility that multiple parentage may occur in Eastern Kingbirds: if females mate with more than one male, then a single brood may include offspring of different fathers. A protein electrophoretic survey was performed to test this possibility and the results are presented elsewhere (McKitrick 1990). Based on these results, recalculations of heritability estimates were possible, and although these recalculations resulted in a substantial decrease in an already small sample, the outcome is suggestive. Removal of cases of doubtful parentage from analyses of heritability had variable effects on the results. The striking increase in h² for females when maternal and ambiguous exclusions are removed suggests that all the ambiguous exclusions may be due to multiple maternity, that is, nest parasitism. However, in all cases of nest parasitism, not only will the resident female not be the mother of all nestlings in her nest, but the resident male also might not be the father of those same nestlings. If this were true, it would be expected that male-offspring heritability estimates should increase when

TABLE 7.   Recalculation of heritabilities omitting exclusion cases.

		Left					Right				
		h²	SE	r²	P	n	h²	SE	r²	P	n
Male parent—	A[1]	0.65	0.38	0.07	0.1	40	−0.02	0.28	0.9⁻⁴	0.95	41
single offspring	B	0.64	0.34	0.06	0.06	59	0.24	0.31	0.01	0.44	55
Female parent—	A	1.20	0.28	0.35	0.0001	36	0.40	0.28	0.06	0.15	33
single offspring		(1.10	0.32	0.27	0.001	35	−0.15	0.33	0.007	0.65)*	32
	B	0.92	0.20	0.28	0.0001	50	0.86	0.26	0.19	0.002	48
		(0.85	0.22	0.24	0.0004	49	0.76	0.31	0.12	0.02)*	47

[1] A = families omitted that had definite paternity (maternity) exclusion or an either-parent exclusion; B = only families omitted with a definite paternity (maternity) exclusion.
* With outlier (Family 13) omitted.

paternity and ambiguous parental exclusions are omitted also, but this did not occur. This supports the possibility that these males are indeed the father of their putative offspring, and that the "parasitized" nests belong to the mate of the parasite (McKitrick 1990). Alternatively, the decrease in significance of heritability based on male parent-offspring regressions could simply be due to the reduction in sample size. More rigorous tests of parentage are necessary to explore this (Burke and Bruford 1987, Quinn et al. 1987, Wetton et al. 1987).

Stabilizing selection tends to reduce genetic variation (Fisher 1930), therefore heritability of traits with a history of strict selective control may be near zero. Based on analyses of laboratory and farm animal populations, it has been suggested that for traits closely related to fitness, such as clutch or brood size, heritability estimates should be very low (Falconer 1960, 1981). Conversely, heritability values significantly different from zero reflect the potential of the trait to respond to natural selection. In wild populations, however, this "rule" does not seem to hold up well, although few quantitative measures have been made for birds. Findlay and Cooke (1982) suggested that synchrony of hatching date is adaptive in the Lesser Snow Goose (*Chen caerulescens caerulescens*), but their heritability estimate was 0.44 (SE = 0.16). They noted this apparent paradox, and suggested that possibly the estimate reflected transient genetic variance and not the variance maintained in the population; alternatively, this high genetic variance could be due to immigration.

Rose (1983) challenged the tenet that fitness traits should have low heritabilities, noting the lack of support for this notion in wild populations of animals, including birds. Certainly fitness traits, that is, traits associated with productivity, have been stressed in agricultural populations and may well have much less genetic variance than such traits in natural populations. However, a study of Collared Flycatchers (*Ficedula albicollis*; Gustafsson 1986) revealed heritability estimates near zero for lifetime reproductive success (0.0083 for males, −0.0142 for females), and a recent study of medium ground finches (*Geospiza fortis*; Gibbs 1988) yielded a low heritability estimate (0.08) for clutch size. These estimates are in keeping with earlier dogma.

There is no question that the estimation of heritability in natural populations is laden with difficulties, both in the theory and the practice. Parental and site environmental correlations, assortative mating, measurement of offspring of different ages, and various types of data manipulations can lead to erroneous estimates (see Hailman 1986, Boag and Van Noordwijk 1987). Multiple paternity is a factor that can influence heritability estimates as well (McKitrick 1990). Furthermore, interpretation of the results is not straightforward (Rose 1983). However, these estimates may nevertheless yield information on the potential of a trait to change, whether through selection or other processes, and they may reveal patterns suggestive of interesting biological phenomena. The results of the present study are not straightforward, although they suggest high heritability for the length of insertion of M. flexor cruris lateralis in Eastern Kingbirds; the significance of this result is strengthened by the results of bootstrapping. The directional asymmetry in this measurement and difference in significance of heritability estimates for the two sides is puzzling, and attempts at explanations can only be speculative at this point. Whereas other traits with high heritabilities have been shown to be under selective control (e.g., Boag and Grant 1981), this asymmetry suggests that muscle size may not be related to fitness. This is probably a reasonable suggestion, as the trait does not appear to be correlated with two estimates of body size (weight and femur length), a trait that presumably is under selective control. If true, this may suggest that variation in size of M. flexor cruris lateralis may be random, possibly involving a relaxation of selection for robust morphology in aerial foragers that use this muscle little or not at all (McKitrick 1986). A sample considerably larger than 27 families is necessary to determine whether the lack of normality in the data is real or artifactual, but this information probably would not substantially alter the conclusions presented herein.

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APPENDIX

Measurements of insertion length and femur length. Data are arranged in the following order: Family number, left male insertion length, left male femur length, right male insertion length, right male femur length, left female insertion length, left female femur length, right female insertion length, right female femur length, offspring 1 left insertion length, etc.; number of parents, number of offspring, approximate age of offspring (in days). Missing data are denoted by -0.

01,1.3,20.05,1.72,19.88,1.50,19.48,0.96,19.30, 1.48,18.66,1.66,18.77,1.02,18.39,0.88,18.20, 2.13,18.14,1.97,17.94,1.17,19.10,2.28,18.76, 2,4,14

02,1.62,19.02,1.54,19.01,0.39,19.01,0.46,19.18, 1.42,19.01,1.71,19.50,-0,-0,-0,-0,-0,-0,-0,-0, -0,-0,-0,-0,2,1,15

03,1.97,19.59,2.01,19.61,1.16,18.86,1.36,18.89, 1.76,19.27,1.90,19.41,1.74,18.79,1.70,18.45, 0.76,19.15,1.11,19.10,1.05,18.59,1.36,19.05, 2,4,14

04,2.29,19.00,2.36,18.73,-0,-0,2.29,19.04,1.87, 16.04,1.80,16.34,2.39,16.52,2.03,16.65,2.12, 15.47,2.12,15.67,1.44,15.94,-0,16.11,2,4,6

05,-0,-0,-0,-0,1.95,18.21,1.90,18.54,1.68,15.95, 1.54,16.30,1.73,16.55,1.70,16.52,1.68,16.98, -0,-0,-0,-0,-0,-0,0,1,3,7

06,1.80,19.34,1.99,19.25,0.89,19.27,1.06,19.47, 2.42,18.44,2.25,18.53,1.88,19.22,2.24,19.39, 1.76,18.14,2.04,18.43,2.06,19.17,2.10,19.32, 2,4,15

07,1.10,19.13,1.98,19.21,2.08,18.98,2.78,18.92, 1.96,15.89,2.20,15.79,-0,-0,1.59,17.15,1.81, 16.95,1.69,16.99,-0,-0,-0,-0,2,3,5

08,1.10,19.33,1.71,19.32,3.18,19.09,-0,-0,1.71, 18.59,2.19,18.67,2.38,18.85,1.76,19.05,1.58, 18.23,1.64,18.53,-0,-0,-0,-0,2,3,13

09,-0,-0,-0,-0,1.32,19.32,1.48,19.16,2.23,17.24, 1.63,17.10,1.75,17.33,1.83,17.34,1.73,17.33, 2.75,17.22,2.12,17.75,2.35,17.91,1,4,7

10,2.49,18.85,2.80,18.85,2.12,18.90,2.07,18.99, 1.70,18.94,1.77,18.94,2.75,19.23,2.34,19.22, 2.44,19.10,2.14,19.27,2.37,18.28,-0,-0,2,4,16

11,2.50,19.11,1.96,19.08,-0,-0,-0,-0,-0,-0,1.64, 19.05,2.48,-0,2.69,18.91,1.14,-0,1.09,19.07, -0,-0,-0,-0,1,3,16

12,1.29,18.33,1.36,18.23,2.07,20.03,1.99,20.09, 2.03,19.53,2.08,19.68,0.93,16.41,1.86,15.45, 1.30,19.33,2.07,19.44,-0,-0,-0,-0,2,3,13

13,-0,-0,-0,-0,3.55,19.41,4.38,19.41,3.11,14.55, 3.33,14.46,-0,-0,-0,-0,-0,-0,-0,-0,-0,-0,-0,1, 1,4

14,2.06,19.55,2.32,19.37,3.59,19.13,3.32,19.05, 1.95,19.30,1.98,19.15,2.87,19.32,3.81,19.23, 2.86,19.16,2.94,19.18,2.84,19.15,3.72,19.16, 2,4,15

15,-0,-0,-0,-0,1.69,18.98,1.32,18.94,2.09,18.82, 2.60,18.75,-0,-0,-0,-0,-0,-0,-0,-0,-0,-0,-0,1, 1,7

16,1.74,19.30,1.82,19.27,1.48,19.96,-0,-0,1.14, 19.34,1.03,19.40,0.76,19.46,0.96,19.52,1.71, 19.47,1.72,19.51,-0,-0,-0,-0,2,3,14

17,1.55,19.84,1.95,19.84,1.81,19.15,2.25,19.03, 2.11,19.89,2.05,19.99,2.25,19.53,2.14,19.50, -0,-0,-0,-0,-0,-0,-0,-0,2,2,16

18,1.69,19.09,1.45,19.23,-0,-0,-0,-0,0.87,18.97, 0.10,19.05,1.78,18.04,1.98,18.08,-0,-0,1.70, 18.92,1.62,18.65,1.49,18.79,1,4,15

19,1.28,19.73,0.62,19.56,2.81,20.40,2.83,20.45, 1.77,19.47,2.0,19.36,2.71,19.01,2.58,19.18, 2.25,18.63,2.56,18.77,-0,-0,-0,-0,2,3,13

20,2.38,19.12,2.70,19.25,2.79,19.82,2.62,19.97, 2.25,18.34,1.66,18.45,1.99,19.12,1.97,19.33, 3.20,18.55,2.74,18.74,-0,-0,-0,-0,2,3,12

21,2.21,18.89,2.38,19.00,1.63,18.91,1.72,18.91,

-0,-0,-0,-0,2.05,18.70,1.10,18.67,2.22,18.65,
-0,18.84,-0,-0,-0,-0,2,3,14
22,1.07,19.04,1.32,18.99,0.94,18.64,2.69,18.98,
1.09,19.59,0.83,19.69,1.03,18.87,1.46,18.78,
-0,-0,-0,-0,-0,-0,-0,-0,2,2,10
23,2.07,20.01,2.25,20.00,1.89,19.59,1.82,19.59,
0.96,19.74,1.46,19.74,1.83,19.58,1.84,19.89,
1.74,19.73,1.90,19.88,1.43,19.61,1.50,19.59,
2,4,-0.
24,1.63,19.09,1.77,19.23,-0,-0,-0,-0,2.42,19.09,
2.53,19.26,1.89,18.32,2.03,18.57,2.41,18.49,
2.42,18.63,-0,-0,-0,-0,1,3,8

25,2.01,19.20,2.10,19.45,0.79,18.30,1.16,18.30,
2.16,17.67,2.21,17.58,-0,-0,-0,-0,-0,-0,-0,-0,
-0,-0,-0,-0,2,2,9
26,1.84,19.25,-0,-0,2.14,20.02,2.35,19.92,2.50,
18.90,2.20,18.94,3.17,19.12,3.33,18.90,2.71,
18.11,2.38,18.01,1.29,18.53,2.28,18.40,2,4,8
27,2.09,18.79,1.86,18.82,2.30,19.23,1.94,19.12,
1.46,18.79,1.77,19.16,-0,-0,1.28,18.35,1.95,
18.50,2.16,18.45,1.47,18.25,-0,-0,2,4,9