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ANALYSIS OF THE GROWTH OF THE NOVA SCOTIA BLANDING'S TURTLE

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Abstract. We have determined that the different plastral scutes (rigid sectional plates found on the plastron, the flat shell structure of a turtle's "belly") of Blanding's turtle grow at different rates, while scute pairs grow homogeneously. Scute width was used as a new growth measurement to model the growth curve of Blanding's turtle by fitting exponential and polynomial models. We discovered that the Nova Scotia population of Blanding's turtles follows the Von Bertalanffy model of growth for plastral scutes. In order to determine how population locations and temperature affect the growth of Blanding's turtle, several statistical modeling techniques are discussed, including linear and non-linear mixed effect models.

1. **Introduction.** Blanding's turtle has an annual record of growth similar to trees, in that growth rings are forged as a growth record. They differ from trees, which have only one set of tree rings, in that they have twelve sets of growth records represented by twelve plastral scutes, each of which grows an additional ring annually. These growth rings are forged until Blanding's turtle reaches sexual maturity (age twenty to twenty-five for the Nova Scotia population). The data studied in this research was collected by Monik Richard, a M.Sc. student under the joint supervision of Dr. Tom Herman and Dr. Soren Bondrup-Nielsen of the Department of Biology, Acadia University. After deleting the "headstart" turtles which lived under optimal light, heat and feeding condition as well as turtles with missing values from the original data set, the data contained 108 turtles. Among these turtles, there are 53 from Kejimkujik National Park (KNP), 16 from McGowan Lake (ML), and 39 from Pleasant River (PR). The variables of this data set include POP, TUR, SCU, AGE, RWIDTH, and YEAR. The variable POP identifies these three locations. The variable TUR refers to the individual unique identification number assigned to each turtle in this study. Growth ring observations were not available on all twelve scutes, but only for the four left and the four right scutes. The top and bottom two scutes were excluded since the wear on the plastron makes ring identification difficult for these locations. These eight remaining scutes were denoted as L2, L3,

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POP	TUR	SCU	AGE	RWIDTH	YEAR
ML	2,3-1,3	L2	0	181.97	1981
ML	2,3-1,3	L2	1	69.03	1982
ML	2,3-1,3	L2	2	23.77	1983

Table 1. A Sample of the Dataset of the Nova Scotia Blanding's Turtle

L4, L5 (left from the back to the front) and R2, R3, R4, R5 (right from the back to the front), and the variable SCU refers to this identification. The variable AGE refers to the ring identification or running age of the turtle when forged. Each turtle may have different numbers of growth rings ordered from the 1^{st} ring to the n^{th} ring. The 1^{st} ring (AGE 0), also called the baseline, is the size of a turtle at hatching. Ring widths in each scute of individual turtles, denoted by RWIDTH, were measured in pixels by the diagonal distance between two growth rings using ImageTool [1], an image analysis shareware software program. More information about the ring width growth measurement can be found in Richard [2]. Finally, the variable YEAR refers to the year the growth ring was forged. Table 1 shows sample records selected from TUR 2,3-1,3 in ML.

Figure 1 displays the boxplots of RWIDTH of all 108 turtles by SCU. The distributions of such ring widths appear strongly right skewed for each scute, with many relatively large values, which are either baseline values or the results of more rapid growth in the turtle's early years. It appears that ring widths are not homogeneous with regard to scute growth, with the boxplots for scutes R5 and L5 being quite different from the rest. In order to test the validity of this observation, a Friedman test on scute-block effects was conducted for each of the 108 turtles. The Friedman test arises in a situation in which responses across t treatments are measured within n blocks, and these responses are then ranked from 1 to t within each block, according to their magnitude. The null hypothesis to be tested is that within each block these vectors of rankings are randomly selected from a set of possible $t!$ values, indicating that there is no pattern of rankings in the blocks, so that there is no difference between the treatments. For this test we take the SCU categories to define the treatments. For each turtle we consider the blocks to be the values of AGE as defined by the location of the rings within each scute, and the responses are the values of RWIDTH for that AGE across SCU. Rejection of the null hypothesis would indicate that for the specified turtle, there is a significant difference in the relative RWIDTH values across the scutes. Overall, for 81 out of 108 turtles there is sufficient evidence at a significance level of 0.001 to conclude that ring widths differ by scute. However, Figure 1 also shows that scute pairs might be homogeneous with regard to ring width distribution. A Sign test was conducted to determine pairwise differences for the four pairs of scutes (L2 and R2, L3 and R3, L4 and R4, L5 and R5). The results of the tests indicate that there is indeed pairwise homogeneity of ring width distributions in the scutes. The detailed results from the Friedman and Sign tests are found in "Analysis of the Blandings Turtle and Climate Change", a consulting report prepared at Acadia University in 2006 by Y. C. Huang and H. Ingo. This report is available from the corresponding author.

The objective of this research is to model the growth curve of Blanding's turtle, and to implement such models in order to examine how climate factors such as temperature affect the growth of Blanding's turtle.

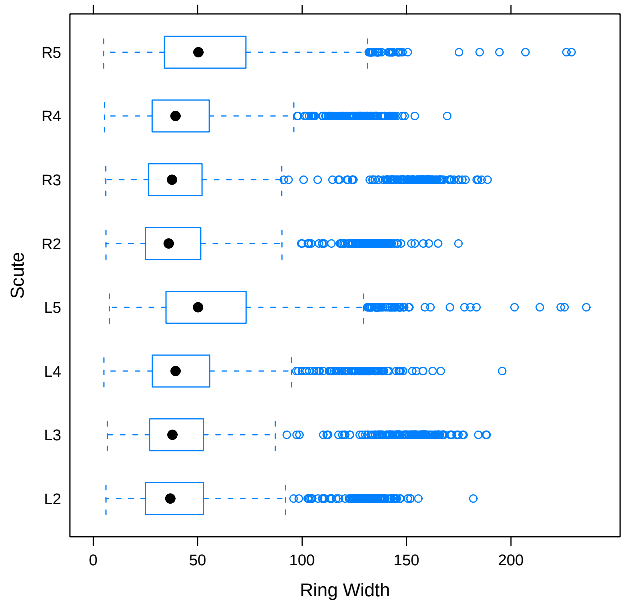

FIGURE 1. Boxplot of the ring widths for the scute comparison.

2. Growth Curve Model.

2.1. **Scute Growth Measurement.** The most commonly used growth measurements in the literatures are carapace length ([3], [4]), which is the length of the top part of the shell, and plastron length, which is the length of the middle line of the flat shell structure on the underside of the turtle ([5], [6]).

Another growth measurement is the ring width which in our case is measured by RWIDTH. For demonstration purposes, Figure 2 plots RWIDTH values by four left scutes of 15 year old TUR 2,3-3,9 from KNP. Although these values exhibit an overall decreasing pattern as the turtle ages, there is present a large variation from year to year.

We note the large ring width values in its baseline (AGE 0), as well as AGE 1 and AGE 2.

In this paper, for an individual turtle's plastral scute, the scute width is defined as

$$SW_t = \sum_{i=0}^{t} RW_i,$$

where RW_i is the i^{th} RWIDTH. Considering the ring width as annual growth, the scute width SW_t measures an accumulative growth up to the t^{th} ring or up to the t^{th} running age ($t = 0, 1, ..., n$). This new measure has the advantage of smoothing the growth curve, as can be observed in Figures 3 and 4.

2.2. **Exponential Growth Model.** The non-homogeneity of growth across scutes with regard to the ring width indicates that the individual plastral scutes of each turtle should be considered as the unit for modeling growth. The left-right pairwise

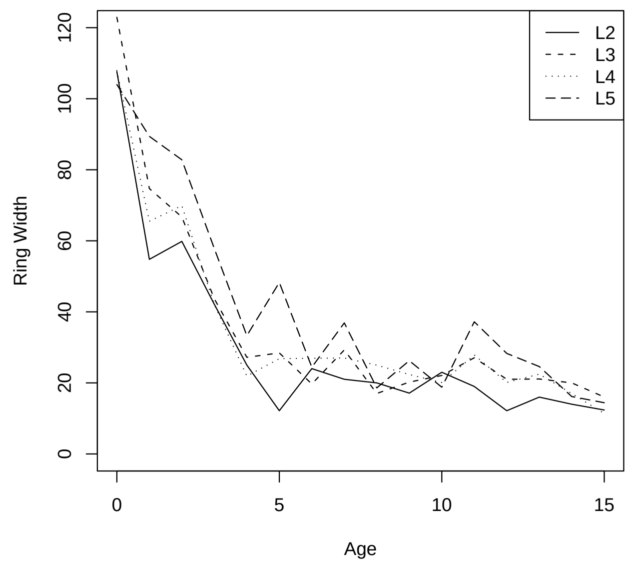

FIGURE 2. Plot of the ring widths by four left scutes of TUR 2,3-3,9 from KNP.

homogeneity indicates that only one-side scutes need to be considered, and in the rest of the paper, only the second left plastral scute (L2) will be used. Figure 3 visualizes scute widths SW_t located in L2 of all 108 turtles, where the sample average values of SW_t at each age are linked by the solid line.

This average SW_t function is fairly smooth, with a shape that may be modelled by an exponential or second order polynomial function. A good candidate for accumulative growth curves is the Von Bertalanffy equation [7]. This equation has been used to model growth of various organisms, particularly in marine science. It has also been used to model plastron length at age t as

$$PL_t = a(1 - be^{rt}) \tag{1}$$

where PL_t is the plastron length at age t, a is the mean asymptotic size in the population, b is a variable related to size at hatching, and r is an intrinsic growth rate ([5], [6], [8]).

Therefore, the scute width SW_t, hereafter referred as VB, the Von Bertalanffy equation, may be written as

$$SW_t = a(1 - be^{rt}) + e_t, \tag{2}$$

where $\{e_t\}$ is a random normal error process with zero mean and a constant variance. If $r < 0$, a is the mean asymptotic scute size at maturity since in this case $\lim E(SW_t) = a$. The parameter b is related to the mean size of the scute at hatching, since when $t = 0$, $E(SW_0) = a(1 - b)$. Therefore the baseline ring width may be estimated by $a(1 - b)$. Finally, r is an intrinsic growth rate of that scute. Because the younger turtles' growth curves may be too short to be estimated, the Von

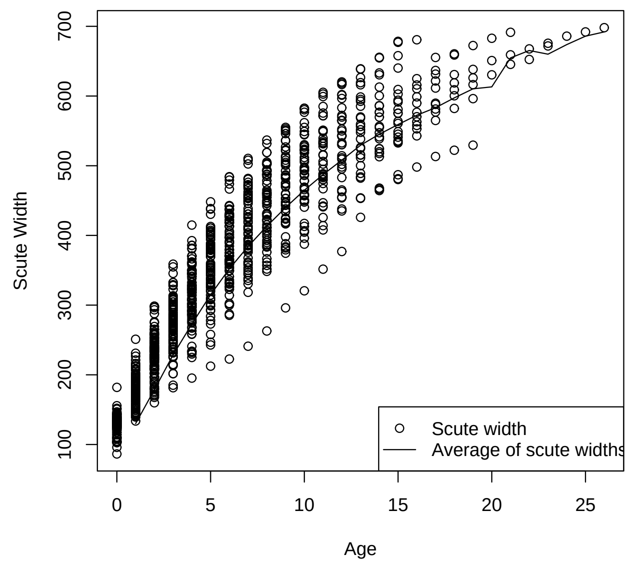

FIGURE 3. Plot of the L2 scute widths versus AGE of all 108 turtles

Bertalanffy model was fitted for the second left scute L2 of twenty-two individual turtles older than 14 from all three populations using the **R** [9] function "nls" [10].

There were four turtles from population KNP, eight turtles from population ML, and ten turtles from population PR. A residual diagnostic check was conducted for each fit. Overall the residuals are fairly normally distributed with constant variances. The autocorrelation plots indicate some autocorrelation dependency at lag one or two in the residual processes, which is quite common in the case of growth measurements or repeated measurements. In order to test for any trend remaining [11], the regular two-sided Kendall's Rank Correlation Coefficient Test on residuals was run in StatXact [12] for individual turtles. Appendix 5.1 shows that the smallest p-value from the tests is 0.3734, indicating that for all 22 turtles there is no trend remaining when modelling by the VB model. Wilder [13] shows that the actual p-values from an improved Kendall's test with autocorrelated errors would be bigger than those in Appendix 5.1 obtained from the regular Kendall's test which assumes independent errors. Therefore it appears safe to believe that the Von Bertalanffy model is adequate for fitting the scute width growth curve. The parameter estimates from the VB fit show that for example, the mature L2 size of Turtle 2,3-3,9 from KNP is $\hat{a} = 757.540$ (se. 9.262), with an estimated baseline scute width of $757.540(1 - 0.8193) = 136.888$ ($\hat{b} = 0.8193$, se. 0.013), which compares well with the observed baseline value of 137.93. The growth after hatching has an intrinsic rate of about -0.128 (se. 0.004). Similarly, the Von Bertalanffy model provides very good fits for other scutes.

2.3. **Polynomial Growth Model.** The polynomial model is commonly used for modelling growth curves, and Figure 3 indicates that such a second order polynomial would provide another option for scute growth. The polynomial equation for scute width SW_t may be written as

$$SW_t = b_0 + b_1 t + b_2 t^2 + e_t \tag{3}$$

where e_t is same as in eqn. (2), while b_0, b_1, and b_2 are coefficients, and t is the ring age.

The second order polynomial model was fitted to the scute width curves for all 22 turtles. The large adjusted R-squared values, a measure of goodness-of-fit, indicate very good fit, with all adjusted R-squared values greater than 0.9. Results from residual diagnostic checks are similar to those for the VB models.

Figure 4 plots the scute widths of L2, and its polynomial and VB fitted curves, for an individual turtle. It is very clear that the VB model provides a more accurate fit than the polynomial model in this case. Most parts of the original growth curve are precisely fitted by the VB model. In fact, this is the case for most of the other individual turtle plots as well, showing that the VB model is the better choice for this data.

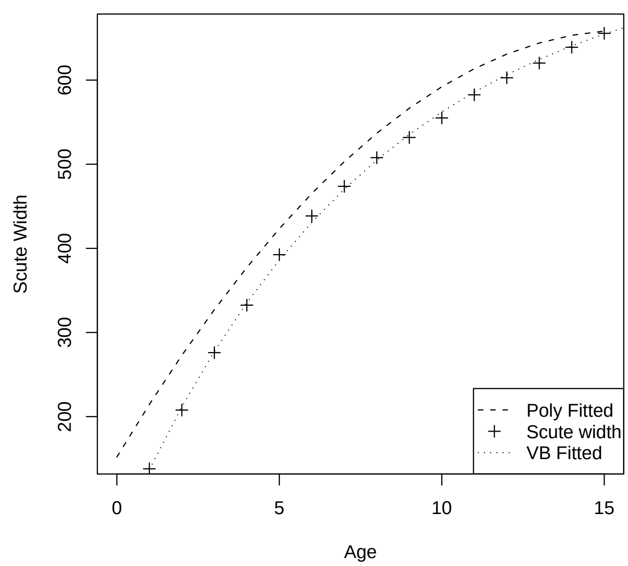

FIGURE 4. Fits of the scute width growth of L2 for TUR 9-1, 8 from KNP. The dashed lines represent the polynomial and VB fits while the cross points represent the raw SW_t values.

The residual standard errors of both models were compared for each turtle with AGE greater than or equal to fifteen (see Appendix 5.2.). Overall the VB model fits have smaller residual standard errors than polynomial models with only a few exceptions, so that one can conclude that the turtle scutes appear to grow exponentially.

3. **Applications and Results.** With the VB model being the appropriate model for the individual turtle scute width curve, it is natural to use a non-linear mixed effect model for all 108 turtles to examine the population impact on growth considering individual turtle random effect. Non-linear mixed effect modeling is a method for repeated measures developed in the early 1990s. A method that combines least square estimates for non-linear fixed effects models and maximum likelihood or restricted maximum likelihood estimates for linear mixed effect models was proposed by Lindstrom and Bates [14]. The flexible covariance structure allows for non-constant correlation among the observations and unbalanced data. Individual responses all follow a similar functional form with parameters that vary among individuals. The basic assumption of this model is that error terms are normally distributed. Following eqn. (2), the model for the SW_{ij}, the scute width up to the age of the j^{th} ring on the i^{th} turtle may be written as

$$SW_{ij} = A_i - B_i e^{r_i j} + e_{ij}, \tag{4}$$

where $A_i = a_i$, $B_i = a_i b_i$ and e_{ij} is a normally distributed noise term with a variance σ^2. The term e_{ij} may be updated to an AR(1) process to capture the autocorrelation. We have tested various combinations of the growth parameters, A, B and r, in terms of population location effects being fixed, and random individual turtle effects. It turns out that the model with A as a fixed population effect, and B and r as fixed population and random individual effects, provides better estimation results for capturing the trend of the scute width growth of all 108 turtles, and yields a relatively larger likelihood function value and smaller values of Bayesian and Akaike information criteria. Since A_i is the mean asymptotic size in the population, this parameter may be mainly affected by population locations. The parameters B_i and r_i are related to the size at hatching and the intrinsic growth rate respectively, which may be affected by both population locations and individuals. That is,

$$A_i = \begin{bmatrix} 1 & X_{i1} & X_{i2} \end{bmatrix} \times \begin{bmatrix} A_0 \\ A_1 \\ A_2 \end{bmatrix} \tag{5}$$

$$B_i = \begin{bmatrix} 1 & X_{i1} & X_{i2} \end{bmatrix} \times \begin{bmatrix} B_0 \\ B_1 \\ B_2 \end{bmatrix} + \mu_{i1}, \tag{6}$$

$$r_i = \begin{bmatrix} 1 & X_{i1} & X_{i2} \end{bmatrix} \times \begin{bmatrix} r_0 \\ r_1 \\ r_2 \end{bmatrix} + \mu_{i2}, \tag{7}$$

where X_{i1} and X_{i2} are two indicators for population locations, and $\mu_i = (\mu_{i1}, \mu_{i2})^T$ is a vector of random effects associated with an individual turtle, $\mu_i \sim N(\mathbf{0}, \sigma^2\mathbf{D})$, and $\sigma^2\mathbf{D}$ is a covariance matrix of μ_i.

This model was implemented under the **R** package "nlme" using the covariance notation detailed in [14] and given above. Let the subscript 0 denote growth parameters for KNP, and subscripts 1 and 2 denote differences of these parameters between ML and KNP, and PR and KNP respectively. With initial values for fixed parameters: A_0, A_1, A_2; B_0, B_1, B_2; r_0, r_1, r_2 as $700, 0, 0$; $700, 0, 0$; $-0.1, 0, 0$, the final estimates are $\hat{A}_0 = 995.570$ (s.e. 35.825), $\hat{A}_1 = -127.246$ (s.e. 40.873), $\hat{A}_2 = -40.406$ (s.e. 41.710); $\hat{B}_0 = 865.558$ (s.e. 35.406), $\hat{B}_1 = -136.844$ (s.e.

40.290), $\hat{B}_2 = -34.117$ (s.e. 41.090); $\hat{r}_0 = -0.063$ (s.e. 0.004), $\hat{r}_1 = -0.011$ (s.e. 0.006), $\hat{r}_2 = 0.001$ (s.e. 0.005). The p-values for testing $A_1 = 0$, $B_1 = 0$ and $r_1 = 0$ are 0.0019, 0.0007 and 0.0472 respectively, providing significant evidence of population location effects between ML and KNP. There was no significant difference between PR and KNP.

The cumulative growth measurement can be easily converted into annual growth by taking differences. The nonlinear exponential growth model also can be easily transformed into a linear model by taking log transformation, such as,

$$\begin{aligned} SW(t) &= a(1 - be^{rt}), \\ \frac{dSW(t)}{dt} &= -abe^{rt}r, \\ \log(\frac{dSW(t)}{dt}) &= \log(-abr) + rt. \end{aligned}$$

Since the difference of scute width is the ring width at AGE t, $\frac{dSW(t)}{dt} \approx RW_t$, this leads to the linear model for the log of ring width

$$\log(RW_t) = \log(-abr) + rt + \epsilon_t. \tag{8}$$

If the error terms ϵ_t are assumed to be normally distributed, then RW_t will have a *lognormal* distribution. The *lognormal* as well as the *gamma* have been used to model biological growth ([15]).

Eqn. (8) provides a linear form for modeling the annual ring growth, an approach used by Van Deusen [16] to analyze tree ring data. Note that the error terms ϵ_t may be additively affected by other covariates, so that they may be further modeled by a multiple regression.

Since we have both the population location information and the annual temperatures available in the data set, one such linear model may be written as

$$\log(RW_t) = \beta_0 + \beta_1\text{Age} + \beta_2\text{Temperature} + \beta_3\text{Pop location} + u_t, \tag{9}$$

assuming u_t is a random error process. To take account of individual effects on the parameter estimation, a linear mixed effect model was conducted for all 108 turtles with an individual turtle random effect. The results show significant age and temperature effects (both p-values are 0.000). The detailed results from this linear approach can be found in Huang [17].

4. **Concluding Remarks.** Given data available on eight different scutes, it is possible to determine that scutes grow at different rates, a fact not previously known. Homogeneity of scute left-right pairs is also shown from the preliminary analysis. For modeling the turtle's growth curve, a new growth measurement, scute width, is introduced. Two growth curve models are fitted, the exponential (VB) model, and the second-order polynomial model. From curve-fitting results and residual diagnostic checks, both appear to be very good candidates for the turtle's scute growth curve model. After comparing these two models through visualizations and residual standard error, the exponential model appears to be the better growth model. Using this selected exponential growth model, some applications are conducted to determine population and temperature effects on turtle growth. The applications include a non-linear mixed model, and a linear mixed effect model with auto-correlation update. As a result, there are some suggested population and temperature effects.

The methods detailed here for the analysis of this data set can be generalized to studies of other types of turtles. However, the findings for the data set in Section 3 may be limited by several factors. First of all, the sample is not randomly selected. Any inference will of course be limited to those Blanding's turtles found in the three populations in Nova Scotia. The sizes of the populations are unbalanced, and the number of mature turtles in the sample is small. The available covariate information that is associated with turtle growth provides fairly limited information on the underlying natural process.

Since temperature data is long-term in nature, it is difficult to draw conclusions about a turtle's relationship with temperature for young turtles. Both histograms of the residuals from the nonlinear mixed model and linear mixed model show some evidences of non-normality, which needs further investigation. Finally, the residuals of both models appear to be autocorrelated with lags other than 1, so that updating the models by higher order auto-correlation error terms may improve the accuracy of the results [18]. The model that incorporates the scute effect may be implemented similarly in the non-linear or linear mixed effect model to include more data.

5. Appendix.

5.1. Kendall's Rank Correlation Coefficient Test Results.

TUR	POP	AGE	p-Value (Res)
TUR 2,3-3,9	KNP	15	0.6901
TUR 9-1,8	KNP	15	1.0000
TUR 9-1,2	KNP	16	0.8393
TUR 10-1,10	KNP	17	0.9405
TUR 2,10-1,3	ML	15	0.8944
TUR 2,3-1,8	ML	15	0.8944
TUR 2,3-1,9	ML	15	0.3734
TUR 2,3-8,9	ML	15	0.8944
TUR 2,3-9,10	ML	18	0.7872
TUR 2,3-8,11	ML	19	0.8202
TUR 2,3-2,9	ML	21	0.9088
TUR 2,3-1,3	ML	23	0.7133
TUR 2,11-1,11	PR	15	0.6259
TUR 3,11-1,8	PR	15	0.9647
TUR 8,11-9,10	PR	15	0.5643
TUR 1,2-2	PR	16	0.6553
TUR 2,9-2,8	PR	17	1.0000
TUR 3,11-1,9	PR	17	0.8228
TUR 3,11-1,10	PR	19	1.0000
TUR 3,11-2,9	PR	19	0.8244
TUR 8,11-1,1	PR	18	1.0000
TUR 2,10-1,2	PR	25	0.5735

5.2. **Comparison of Residual Standard Errors between the Polynomial Model and the VB Model.**

Turtle	Population	Age	RSE (Poly)	RSE (VB))
TUR 2,3-3,9	KNP	15	13.25	10.63
TUR 9-1,8	KNP	15	11.43	5.195
TUR 9-1,2	KNP	16	12.01	12.52
TUR 10-1,10	KNP	17	8.173	8.507
TUR 2,10-1,3	ML	15	11.9	11.85
TUR 2,3-1,8	ML	15	13.37	11.29
TUR 2,3-1,9	ML	15	13.87	11.48
TUR 2,3-8,9	ML	15	9.566	8
TUR 2,3-9,10	ML	18	10	10.3
TUR 2,3-8,11	ML	19	7.194	8.027
TUR 2,3-2,9	ML	21	13.49	11.8
TUR 2,3-1,3	ML	23	12.97	11.42
TUR 2,11-1,11	PR	15	13.28	13.39
TUR 3,11-1,8	PR	15	7.621	7.624
TUR 8,11-9,10	PR	15	8.734	7.624
TUR 1,2-2	PR	16	6.507	8.196
TUR 2,9-2,8	PR	17	6.529	6.509
TUR 3,11-1,9	PR	17	9.007	7.148
TUR 3,11-1,10	PR	19	10.33	11.15
TUR 3,11-2,9	PR	19	12.39	8.579
TUR 8,11-1,1	PR	18	10.08	8.88
TUR 2,10-1,2	PR	25	10.62	7.724

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