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DIET OF *CONTOMASTIX VACARIENSIS* (SQUAMATA: TEIIDAE) IN THE GRASSLANDS OF THE ARAUCARIA PLATEAU, SOUTHERN BRAZIL

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***Abstract*.—We analyzed the diet of the teiid lizard Lagarto-Pintado (*Contomastix vacariensis* = *Cnemidophorus vacariensis*) in the high-elevation grasslands of the Araucaria Plateau, southern Brazil, over two years (September 2004-August 2006). Of 232 individuals examined, 175 contained food. We identified prey to categories and summarized them by number (N), volume (V), frequency (F), and importance value index (IVI). In the first year, we surveyed seasonal invertebrate availability. We applied Kolmogorov-Smirnov tests and Spearman's correlations to evaluate diet availability relationships, Permutational Multivariate Analysis of Variance (PERMANOVA) to compare diet composition among sex, age class, season, and year, and a second PERMANOVA to test effects on number of prey (NP), largest prey length (LL), mean prey length (ML), and mean prey volume (MV). We assessed effects of snout-vent length (SVL) and mouth opening (MO) on dietary variables with RRPP, followed by univariate models. We recorded 838 items in 22 categories. Insect eggs, Araneae, and Orthoptera dominated numerically; Blattodea, Araneae, and Orthoptera by volume. Diet differed from environmental availability in all seasons of the first year. Diet composition showed no effects of sex, age class, season, or year. NP and LL were higher in the second year, whereas ML and MV showed no significant variation. SVL correlated positively with LL, ML, and MV, but not NP; MO had no independent effect. Both sexes and age classes increased prey size in the second year, likely reducing demographic differences. *Contomastix vacariensis* is a generalist consumer with selective use of available prey, maintaining a stable trophic structure, and with prey dimensions strongly constrained by body size.**

Key Words.—Brazilian lizard; endemic; food; temperate habitat.

INTRODUCTION

Dietary studies are essential for understanding lizard autoecology, as they can reveal aspects of population dynamics, including intrapopulation variation in prey consumption (Silva and Araújo 2008). For instance, dietary differences between adult males and females often result from sexual dimorphism in head dimensions, such as in the Western Whiptail (*Aspidoscelis tigris* = *Cnemidophorus tigris*; Best and Gennaro 1985) and the South American Clawed Gecko (*Gonatodes humeralis*; Miranda and Andrade 2003). Additionally, ontogenetic dietary shifts are common and are typically attributed to morphological differences between juvenile and adult Lagarto-Verde (*Teius oculatus*; Capellari et al. 2007). Seasonal dietary variation may also occur, influenced by fluctuations in prey availability (e.g., Best and Gennaro 1985; Rodríguez and Casas-Andreu 2011) or due to plasticity in foraging strategy (e.g., the Roughtail Rock Agama, *Laudakia stellio*; Lo Cascio et al. 2001). Understanding these dynamics can provide insights into how population groups of different sexes and age classes share resources, as well as how species respond to environmental pressures, particularly for endemic species with restricted distributions.

Lagarto-Pintado (*Contomastix vacariensis* = *Cnemidophorus vacariensis*; Feltrim and Lema 2000) is a teiid lizard apparently endemic to the Araucaria Plateau in southern Brazil (Stahnke et al. 2006; Souza Filho 2013). It inhabits high elevation grasslands with an apparently homogeneous physiognomy, yet harboring high species diversity, near mixed ombrophilous forests dominated by the pine tree Pinheiro-do-Paraná (*Araucaria angustifolia*; Rezende-Pinto et al. 2009). Individuals are typically found in shallow burrows on rocky outcrops, where they shelter, thermoregulate, and spend most of their active time (Caruccio et al. 2010). The species exhibits sexual dimorphism with females larger than males, but males have relatively longer heads (Rezende-Pinto et al. 2009).

Classified as vulnerable in the Brazilian Red List of Threatened Fauna (Ministério do Meio Ambiente 2022), *C. vacariensis* faces habitat degradation as its primary threat. Despite its conservation status, few studies have investigated its natural history, with research focusing on reproduction (Rezende-Pinto et al. 2009), microhabitat use (Caruccio et al. 2010), and thermal biology and daily activity (Caruccio et al. 2011). Dietary information, however, remains scarce. Preliminary results suggest that *C. vacariensis* consumes few termites, contrasting with other teiid lizards, such as Lagarto-da-Cauda-Verde (*Glaucomastix littoralis* = *Cnemidophorus littoralis*; Menezes et al. 2006), Lagartinho-de-Linhares (*Ameivula nativo* = *C. nativo*; Menezes et al. 2008), and Spix's Whiptail (*A. ocellifera* = *C. ocellifer*; Zanchi-Silva et al. 2020).

In addition, although sexual dimorphism in body and head dimensions has been reported for this species (Rezende-Pinto et al. 2009), no study has yet tested whether such morphological variation is associated with differences in diet. Exploring these potential associations between body size, mouth opening, and dietary traits provides a novel perspective on the trophic ecology of *C. vacariensis*. We evaluated the diet of *C. vacariensis* in high-elevation grasslands near Vacaria, Rio Grande do Sul, southern Brazil. Specifically, we attempted to answer the following questions: (1) What is the diet composition of *C. vacariensis* in the Araucaria Plateau grasslands? (2) Does its diet differ seasonally from prey available in the habitat during the first year of study? (3) Does the diet vary based on sex, ontogeny, season (spring, summer, autumn, and winter), or year? (4) Do the number of prey consumed (NP), the length of the largest prey (LL), and the mean prey length (ML) and mean prey volume (MV) differ by sex, age class, season, or year? (5) Are NP, LL, ML, and MV associated with snout vent-length (SVL) and size of mouth opening (MO)?

Materials and Methods

Study area.—Sampling took place on a private property in Vacaria municipality, within the Campos de Cima da Serra region, Rio Grande do Sul, southern Brazil. The study area is situated at approximately 950 m in elevation and features rocky outcrops inhabited by *C. vacariensis*. Vegetation in the area primarily consists of mixed ombrophilous forest dominated by *Araucaria angustifolia*, with shrubs and high-elevation grasslands (Rezende-Pinto et al. 2009). The region has a humid temperate climate, with mean annual temperature of approximately 15° C and mean annual rainfall of around 1,400 mm (Rezende-Pinto et al. 2009).

Lizards and invertebrate sampling.—We sampled lizards monthly between September 2004 and August 2006, with one-day sampling events conducted each month. We performed active searching from 0800 to 1800 and captured specimens by hand on rocky outcrops in grassland areas. We euthanized lizards using a ketamine-based veterinary anesthetic (Rezende-Pinto et al. 2009) and measured their snout-vent length (SVL) and mouth opening (MO) using a digital caliper (± 0.02 mm). We preserved all specimens in ethanol and deposited them in the scientific collection of the Laboratory of Herpetology at the Federal University of Rio Grande do Sul (UFRGS).

We conducted invertebrate sampling alongside lizard collection during the first year of the study. We captured soil-dwelling invertebrates using pitfall traps placed near the lizard sampling areas. Each trap consisted of a plastic container (10 cm diameter, 20 cm deep) filled with a 10% formaldehyde solution (Southwood 1966). We arranged 12 traps in four rows, with three traps per row spaced 20 m apart. We checked traps monthly, at which time we collected the invertebrates and replenished the formaldehyde solution.

Stomach content analysis.—We analyzed the stomach contents of *Contomastix vacariensis* specimens using a stereomicroscope. We quantified and classified prey items or identifiable fragments to the Order level. We measured the length and width of intact or partially intact prey using a digital caliper (± 0.02 mm). We then calculated dietary metrics, including abundance (N), volume (V), frequency of occurrence (F), and an importance value index (IVI). We determined abundance by counting prey items, and we calculated volume using the spheroid formula (Dunham 1983):

$$V = \frac{4}{3\Pi(L)(W)^2}$$

where L is prey length and W is prey width. We defined the frequency of occurrence as the proportion of stomachs containing each prey category, and we calculated the IVI as the average of the proportions of N, V, and F (Acosta 1982).

For each lizard, we also recorded the total number of prey items consumed (NP), the length of the largest prey item (LL), and we calculated the mean prey length (ML) and mean prey volume (MV). We computed ML and MV from the three largest measurable prey items per individual and estimated them only for individuals that had consumed at least three prey. Following Rezende-Pinto et al. (2009), we classified lizards with SVL ≥ 57.4 mm (females) or SVL ≥ 48.8 mm (males) as adults.

Data analysis.—To assess whether the diet of *Contomastix vacariensis* differed seasonally from prey available in the environment during the first year of the study, we applied three complementary approaches. First, we used Kolmogorov-Smirnov Tests (Zar 1999) to compare seasonal differences in N, V, and F between prey consumed by lizards and prey availability. Second, we evaluated the association between the number of prey consumed and invertebrate availability using Spearman's Rank Correlation (Zar 1999). Third, we calculated dietary niche breadth, based on number of prey consumed across all seasons in the first year, using the reciprocal form of Simpson's Diversity Index (Colwell and Futuyma 1971):

$$B = \frac{1}{\sum_{i=1}^{n} p_i^2}$$

where n is the total number of prey consumed and p_i is the proportion of prey category *i* (Pianka 1966). We standardized the values by dividing *B* by the number of prey categories per season for seasonal comparisons (Levins 1968).

Because data were non-normal and heteroscedastic, we performed a Permutational Multivariate Analysis of Variance (PERMANOVA; Anderson 2001) to evaluate whether diet composition varied according to sex, age class, season, and year, using the adonis2() function from the vegan R package. We constructed a multivariate response matrix based on the number of prey items consumed per taxonomic category and treated missing values in prey categories as zeros, as they indicated absence of consumption. We calculated dissimilarities between individuals using Euclidean distances, tested marginal effects and assessed statistical significance using 999 permutations.

Similarly, to evaluate whether the sex, age class, season, and year affected NP, LL, ML, and MV, we conducted two separate PERMANOVAs using the adonis2() function of R package vegan. One model assessed NP and LL, and the other assessed ML and MV. This separation was necessary because NP and LL were available for all individuals, whereas ML and MV were only available for individuals that had consumed at least three prey items. All response variables were standardized (z-scores) prior to analysis. We used Euclidean distances and 999 permutations, testing marginal effects in both models. To better understand which of the response variables contributed to the multivariate pattern, we performed post hoc univariate comparisons using Mann-Whitney Tests.

To assess whether NP, LL, ML, and MV were associated with SVL and MO, we applied a multivariate approach based on residual randomization (Collyer and Adams 2018). Prior to this analysis, we assessed potential collinearity between SVL and MO using Spearman's Rank Correlation (Zar 1999). The resulting coefficient indicated a strong positive association (r_s = 0.77, $P < 0.001$). Nevertheless, both SVL and MO were included as continuous predictors in the RRPP model to evaluate their individual contributions to variation in the multivariate dietary dataset.

We implemented a linear model with Residual Permutation Procedure (RRPP) using the lm.rrpp() function from the RRPP R package (Collyer and Adams 2018). Dietary variables were standardized (z-scores) to avoid scale effects, whereas SVL and MO were retained in their original units to maintain biological interpretability. Statistical significance was assessed using 999 permutations.

To explore which dietary variables were most strongly associated with relevant morphological predictors, we conducted separate univariate RRPP models for each predictor, conditional on its contribution in the multivariate analysis (Collyer and Adams 2018). These models followed the same residual randomization procedure, with dietary variables standardized as in the multivariate analysis. We performed all analyses in R platform (R Core Team 2020).

Results

We analyzed 232 specimens of *Contomastix vacariensis*, of which 130 individuals we collected between September 2004 and August 2005, and 102 between September 2005 and August 2006. Stomach contained food items in 175 individuals: 62 adult males; 53 adult females; 59 juveniles; and one undetermined specimen (excluded from analyses

Table 1. Diet of Lagarto-Pintado (*Contomastix vacariensis*) in the grasslands of the Araucaria Plateau, Vacaria, southern Brazil, based on 175 specimens collected between September 2004 and August 2006. Values for number of prey items (N), volume (V), frequency of occurrence (F) are expressed as percentages. Importance value index (IVI) represents the mean of the percentage values of N, V, and F. The abbreviation UA = unidentified arthropods.

Food Items	N (%)	V (%)	F (%)	IVI
Mollusca				
Gastropoda	0.12	0.03	0.57	0.24
Arachnida				
Acari	0.12	0.00	0.57	0.23
Araneae	14.68	19.20	46.29	26.72
Scorpiones	1.79	5.61	8.00	5.13
Opilionida	0.12	0.08	0.57	0.26
Hexapoda				
Blattodea	4.77	37.82	18.29	20.29
Coleoptera	1.07	0.68	4.00	1.92
Diptera	0.36	0.63	1.71	0.90
Hemiptera	0.60	2.27	2.86	1.91
Hymenoptera	7.52	1.27	14.29	7.69
Isoptera	0.36	0.01	0.57	0.31
Mantodea	0.24	0.17	1.14	0.52
Orthoptera	11.69	18.35	35.43	21.82
Insect egg	47.26	0.98	6.29	18.17
Insect larvae	0.48	0.41	2.29	1.06
Colleoptera larvae	0.24	0.30	1.14	0.56
Lepidoptera larvae	0.24	1.46	0.57	0.76
Insect ootheca	1.31	6.21	4.57	4.03
Insect pupae	0.12	1.05	0.57	0.58
Mineral material	2.39	1.42	11.43	5.08
Plant material	1.67	0.60	8.00	3.42
UA	2.86	1.44	–	–
∑	100	100	–	–

involving sex or ontogenetic comparisons). We excluded the remaining 57 specimens because their stomachs were empty.

We identified 838 prey items belonging to 22 categories (Table 1). Insect eggs, Araneae, and Orthoptera dominated numerically, whereas Blattodea, Araneae, and Orthoptera contributed the highest proportions to total ingested volume (Table 1). Araneae, Orthoptera, and Blattodea ranked highest in both F and IVI (Table 1). Comparisons between environmental availability and diet composition in the first study year revealed significant differences in all seasons (winter, $D = 0.636$, $P = 0.002$; spring, $D = 0.652$, $P = 0.002$; summer, $D = 0.818$, $P = 0.003$; autumn, $D = 0.783$, $P = 0.001$). No significant correlations were found between prey availability and prey consumption in any season ($r_s = -0.40$ to 0.55, all Ps > 0.05).

In the first year, overall prey availability was highest in summer (n = 14,420), followed by spring (n = 10,389), autumn (n = 9,243), and winter (n = 5,685; Appendix Table 1). Collembola, Hymenoptera, and Diptera dominated environmental samples during winter and spring; however, *C. vacariensis* primarily consumed Hymenoptera, Orthoptera, and Araneae in winter, and Araneae, Orthoptera, and Coleoptera in spring (Appendix Table 1). During summer and autumn, the environment was dominated by Hymenoptera, Collembola, and Araneae, yet the diet was dominated by Orthoptera, Araneae, and Blattodea in summer, and Orthoptera, Hymenoptera, and Blattodea in autumn (Appendix Table 1). Dietary niche breadth (B_S) peaked in summer ($B_S = 0.68$), followed by spring ($B_S = 0.43$), autumn ($B_S = 0.37$), and winter ($B_S = 0.32$).

Diet composition did not differ significantly based on sex, age class, season, or year (all Ps > 0.200). Given the absence of a temporal effect, data from both years were pooled. Juveniles ingested 154 prey items from 15 categories, mainly Araneae, Orthoptera, and Hymenoptera in terms of N, F, and IVI, while Araneae, Orthoptera, and Blattodea accounted for the largest volumes (Table 2). Adults consumed 683 items from 21 categories, with insect eggs, Araneae, and Orthoptera dominating numerically. Blattodea, Araneae, and Orthoptera had the highest V, whereas Araneae, Orthoptera, and Blattodea ranked highest in F. In terms of IVI, Blattodea, insect eggs, and Araneae were most representative (Table 2).

Adult females consumed 524 prey items across 12 categories. Insect eggs, Hymenoptera, and Araneae dominated numerically, while Blattodea, Araneae, and Orthoptera contributed the most in V. Araneae, Blattodea, and Orthoptera showed the highest F, and Blattodea, insect eggs, and Araneae were most important in IVI (Table 3). Males consumed 159 prey items from 20 categories. Araneae and Orthoptera were the most frequent in N, followed by insect eggs, and Blattodea. In terms of volume, Blattodea, Orthoptera, and Araneae prevailed, while Araneae, Orthoptera, and Blattodea showed the highest F and IVI (Table 3).

In winter, lizards consumed 116 prey items from 15 categories, with Hymenoptera, Araneae, and Orthoptera predominating numerically, whereas

Table 2. Diet of juvenile and adult Lagarto-Pintado (*Contomastix vacariensis*) in the grasslands of the Araucaria Plateau, Vacaria, southern Brazil, based on specimens collected between September 2004 and August 2006. Values for number of prey items (N), volume (V), frequency of occurrence (F) are expressed as percentages. Importance value index (IVI) represents the mean of the percentage values of N, V, and F. The abbreviation UA = unidentified arthropods.

Food Items	Juveniles (n = 59)				Adults (n = 115)			
	N (%)	V (%)	F (%)	IVI	N (%)	V (%)	F (%)	IVI
Mollusca								
Gastropoda	–	–	–	–	0.15	0.03	0.87	0.35
Arachnida								
Acari	0.65	0.00	1.69	0.78	–	–	–	–
Araneae	40.26	45.96	52.54	46.25	8.93	16.17	43.48	22.86
Scorpiones	1.95	4.58	5.08	3.87	1.76	5.99	9.57	5.77
Opilionida	–	–	–	–	0.15	0.09	0.87	0.37
Hexapoda								
Blattodea	3.25	6.13	8.47	5.95	5.12	43.91	23.48	24.17
Coleoptera	1.95	2.53	5.08	3.19	0.88	0.45	3.48	1.60
Diptera	0.65	0.02	1.69	0.79	0.29	0.74	1.74	0.93
Hemiptera	1.30	0.43	3.39	1.71	0.44	2.63	2.61	1.89
Hymenoptera	7.79	2.49	15.25	8.51	7.47	1.15	13.91	7.51
Isoptera	–	–	–	–	0.44	0.01	0.87	0.44
Mantodea	–	–	–	–	0.29	0.21	1.74	0.75
Orthoptera	31.82	32.97	44.07	36.29	7.03	12.90	30.43	16.79
Insect egg	–	–	–	–	57.98	1.16	9.57	22.90
Insect larvae	0.65	0.16	1.69	0.83	0.44	0.47	2.61	1.17
Colleoptera larvae	0.65	0.48	1.69	0.94	0.15	0.29	0.87	0.43
Lepidoptera larvae	–	–	–	–	0.29	1.73	0.87	0.96
Insect ootheca	1.30	1.13	3.39	1.94	1.32	7.19	5.22	4.57
Insect pupae	–	–	–	–	0.15	1.25	0.87	0.75
Mineral material	0.65	0.10	1.69	0.81	2.78	1.67	16.52	6.99
Plant material	0.65	0.72	1.69	1.02	1.90	0.60	11.30	4.60
UA	6.49	2.30	–	–	2.05	1.38	–	–
∑	100	100	–	–	100	100	–	–

Blattodea, Scorpiones, and Orthoptera contributed most in V. Araneae, Orthoptera, and Hymenoptera showed the highest F and IVI (Appendix Table 2). In spring, 490 prey items from 16 categories were recorded, with insect eggs, Araneae, and Blattodea most abundant in N. Blattodea, Araneae, and insect ootheca accounted for the greatest volumes, while Araneae, Blattodea/Orthoptera, and plant material had the highest F. IVI values indicated that Araneae, insect eggs, and Blattodea dominated the diet in spring (Appendix Table 2). In summer, 112 prey items from 12 categories were consumed. Insect eggs, Araneae/Orthoptera, and Blattodea were the most frequent in N, while Orthoptera, Blattodea, and Araneae contributed most in V. Araneae, Orthoptera, and Blattodea had the highest F, and IVI values were greatest for Orthoptera, Araneae, and Blattodea (Appendix Table 2). In autumn, 120 prey items were consumed across 15 categories. Orthoptera, insect eggs, and Araneae dominated numerically, whereas Orthoptera, Blattodea, and Araneae predominated volumetrically. Orthoptera, Araneae, and mineral material exhibited the highest F, while Orthoptera, Araneae, and insect eggs dominated in IVI (Appendix Table 2).

The PERMANOVA testing the effects of sex, age class, season, and year on NP and LL revealed no significant differences among sexes, age classes,

Table 3. Diet of adult female and male Lagarto-Pintado (*Contomastix vacariensis*) in the grasslands of the Araucaria Plateau, Vacaria, southern Brazil, based on specimens collected between September 2004 and August 2006. Values for number of prey items (N), volume (V), frequency of occurrence (F) are expressed as percentages. Importance value index (IVI) represents the mean of the percentage values of N, V, and F. The abbreviation UA = unidentified arthropods.

Food Items	Females (n = 53)				Males (n = 62)			
	N (%)	V (%)	F (%)	IVI	N (%)	V (%)	F (%)	IVI
Mollusca								
Gastropoda	–	–	–	–	0.63	0.07	1.61	0.77
Arachnida								
Acari	–	–	–	–	–	–	–	–
Araneae	5.34	17.73	33.96	19.01	20.75	13.96	51.61	28.78
Scorpiones	1.15	4.46	9.43	5.01	3.77	8.14	9.68	7.20
Opilionida	–	–	–	–	0.63	0.22	1.61	0.82
Hexapoda								
Blattodea	4.39	55.84	30.19	30.14	7.55	27.08	17.74	17.46
Coleoptera	0.95	0.71	5.66	2.44	0.63	0.08	1.61	0.77
Diptera	–	–	–	–	1.26	1.79	3.23	2.09
Hemiptera	–	–	–	–	1.89	6.33	4.84	4.35
Hymenoptera	8.40	1.55	18.87	9.61	4.40	0.59	9.68	4.89
Isoptera	–	–	–	–	1.89	0.02	1.61	1.17
Mantodea	0.19	0.26	1.89	0.78	0.63	0.12	1.61	0.79
Orthoptera	2.86	6.77	22.64	10.76	20.75	21.54	37.10	26.47
Insect egg	70.42	0.18	13.21	27.94	16.98	2.55	6.45	8.66
Insect larvae	0.19	0.16	1.89	0.74	1.26	0.91	3.23	1.80
Colleoptera larvae	–	–	–	–	0.63	0.69	1.61	0.98
Lepidoptera larvae	0.38	2.96	1.89	1.74	–	–	–	–
Insect ootheca	0.76	4.87	3.77	3.14	3.14	10.46	6.45	6.69
Insect pupae	–	–	–	–	0.63	3.00	1.61	1.75
Mineral material	2.29	2.24	22.64	9.06	4.40	0.86	11.29	5.52
Plant material	0.76	0.15	7.55	2.82	5.66	1.24	14.52	7.14
UA	1.91	2.13	–	–	2.52	0.33	–	–
∑	100	100	–	–	100	100	–	–

or seasons, but detected a significant effect of year (Table 4). PCA of NP and LL, however, indicated no clear separation between years, as individuals points from both periods largely overlapped in multivariate space (Fig. 1). There was significant interannual variation in NP ($W = 2358.5$, $P < 0.001$) and LL ($W = 2945.5$, $P = 0.021$). NP had a median of 1.00 (IQR = 2.00, Q1 = 1.00, Q3 = 3.00) in the first year and 3.00 (IQR = 3.00, Q1 = 1.00, Q3 = 4.00) in the second year (Fig. 2). LL had a median of 8.00 mm (IQR = 9.25 mm, Q1 = 5.75 mm, Q3 = 15.00 mm) in the first year and 10.00 mm (IQR = 8.00 mm, Q1 = 7.00 mm, Q3 = 15.00 mm) in the second (Fig. 3). This increase was consistent across sexes and age classes. ML and MV did not differ significantly with respect to any predictor, including year (Table 4).

Finally, RRPP multivariate analysis testing the combined influence of SVL and MO on dietary variables (NP, LL, ML, and MV) indicated a significant effect of SVL ($F_{1,58} = 6.98$, $P = 0.002$, $r^2 = 0.107$), but no significant effect of MO ($F_{1,58} = 0.34$, $P = 0.786$, $r^2 = 0.005$). Given these results, we performed univariate RRPP models with SVL as the sole predictor to identify the dietary variables most strongly associated with body size. SVL was significantly associated with LL, ML, and MV, but not with NP (Table 5; Fig. 4).

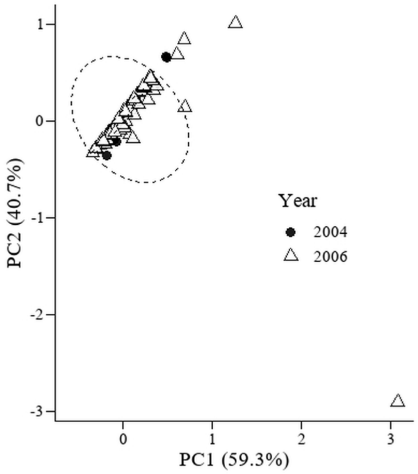

Figure 1. Principal Components Analysis of the diet of Lagarto-Pintado (*Contomastix vacariensis*) in the grasslands of the Araucaria Plateau, Vacaria, southern Brazil, based on the number of prey (NP) and length of the largest prey (LL) of individuals collected between September 2004 and August 2006. The abbreviations PC1 = principal component 1 and PC2 = principal component 2.

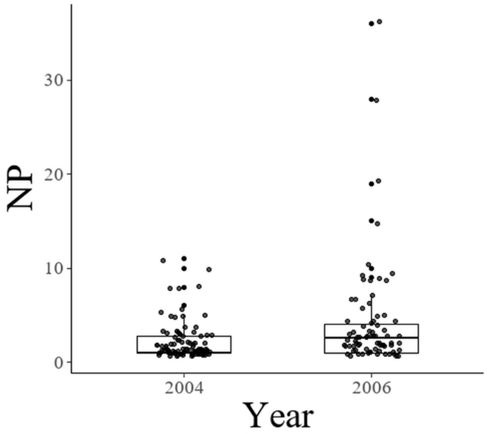

Figure 2. Variation in the median number of prey (NP) consumed by Lagarto-Pintado (*Contomastix vacariensis*) between the two study years in the grasslands of the Araucaria Plateau, Vacaria, southern Brazil, based on specimens collected between September 2004 and August 2006. An extreme value (NP = 302) was excluded to improve data visualization. Horizontal lines are medians, vertical lines are range of values, the box is the first and third quartiles, and black dots are data points and outliers.

Discussion

Contomastix vacariensis feeds predominantly on insect eggs, Araneae, and Orthoptera in the grasslands of the Araucaria Plateau of southern Brazil. Except for the consumption of insect eggs, our findings are consistent with previous studies on teiid lizard diets from different environments. For example, *Ameivula ocellifera* consumed Araneae as the second most important prey item in a Brazilian Restinga (Albuquerque et al. 2018), and Orthoptera as the third most important prey in a Caatinga habitat (Mesquita and Colli 2003). Similarly, Orthoptera was also reported as the third most consumed prey item by the Rainbow Whiptail (*Cnemidophorus lemniscatus*) in the Brazilian Caatinga (Mesquita and Colli 2003). On the other hand, our results contrast with studies which often report termites and/or insect larvae as primary food items for teiids, for example, the Many-lined Whiptail (*Aspidoscelis lineatissima* = *Cnemidophorus lineattissimus*; Rodríguez and Casas-Andreu 2011), Eastern Spotted Whiptail (*A. gularis* = *C. gularis*; Ayala-Flores and Hernández-Salinas 2016), and *Ameivula ocellifera* (Zanchi-Silva et al. 2020). According to Huey and Pianka (1981), active foraging lizards such as teiids typically consume aggregated prey due to their ability to search for food items unavailable to other predators. Our invertebrate sampling during the first year, however,

Table 4. Summary of the Permutational Multivariate Analysis of Variance (PERMANOVA) testing whether the diet of Lagarto-Pintado (*Contomastix vacariensis*) varied according to year and the interaction between sex, age class, and season, based on two sets of dietary variables: number of prey consumed (NP) and length of the largest prey (LL) and mean prey length (ML) and mean prey volume (MV). We conducted analyses using specimens collected in the grasslands of the Araucaria Plateau, Vacaria, southern Brazil, between September 2004 and August 2006.

Predictors	df	Sum of Squares	r^2	F	P-value
		NP and LL			
Year	1	5.47	0.016	2.841	0.045
Sex×Age×Season	3	1.01	0.003	0.176	0.972
Residual	156	300.4	0.873		
Total	172	344.0	1.000		
		ML and MV			
Year	1	1.06	0.008	0.588	0.519
Sex×Age×Season	2	0.487	0.004	0.136	0.923
Residual	48	86.2	0.684		
Total	63	126.0	1.000		

Table 5. Summary of univariate Residual Randomization Permutation Procedure (RRPP) testing whether four dietary variables, (1) number of prey (NP), (2) length of the largest prey (LL), (3) mean prey length (ML), and (4) mean prey volume (MV) were associated with body size (SVL) in Lagarto-Pintado (*Contomastix vacariensis*) from the grasslands of the Araucaria Plateau, Vacaria, southern Brazil, based on specimens collected between September 2004 and August 2006.

Response Variable	df	r^2	F	Z	P-value
NP	1	0.020	1.18	0.51	0.311
LL	1	0.181	12.86	2.69	0.002
ML	1	0.103	6.69	2.07	0.012
MV	1	0.124	8.30	2.45	0.004

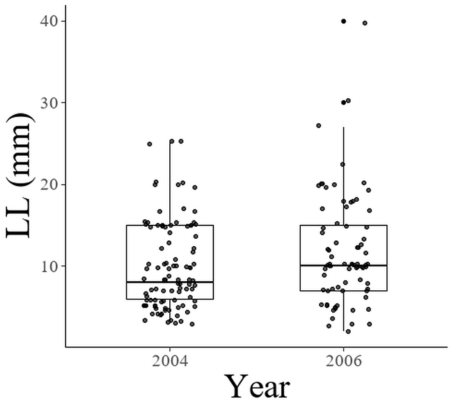

Figure 3. Variation in mediane length of the largest prey (LL) consumed by Lagarto-Pintado (*Contomastix vacariensis*) between the two study years in the grasslands of the Araucaria Plateau, Vacaria, southern Brazil, based on specimens collected between September 2004 and August 2006. Horizontal lines are medians, vertical lines are range of values, the box is the first and third quartiles, and black dots are data points and outliers.

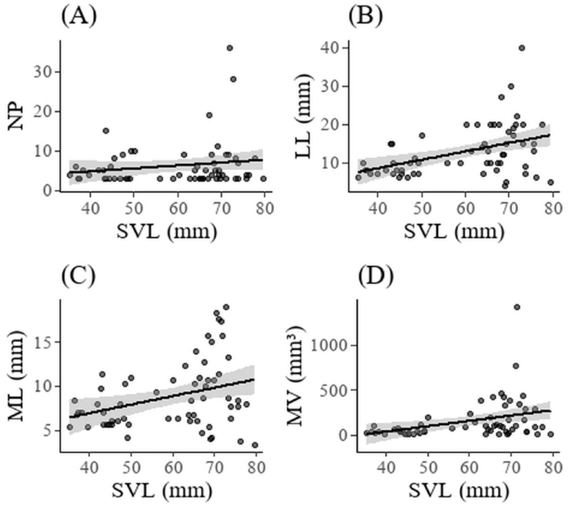

Figure 4. Relationships between snout-vent length (SVL) and four dietary variables in Lagarto-Pintado (*Contomastix vacariensis*): (A) number of prey (NP), (B) length of the largest prey (LL), (C) mean prey length (ML), and (D) mean prey volume (MV). Data are based on specimens collected between September 2004 and August 2006 in the grasslands of the Araucaria Plateau, Vacaria, southern Brazil. An extreme value (NP = 302) was excluded to improve data visualization. Shaded areas are the 95% confidence band.

revealed a low abundance of termites, while insect larvae were consistently present. Thus, the absence of termites in the diet of *C. vacariensis* likely reflects their scarcity in high-elevation grasslands, whereas the limited use of insect larvae, which were available at low levels year-round, suggests they are not a preferred resource.

The substantial consumption of insect eggs by *C. vacariensis* is noteworthy, as prior studies have documented these items as negligible in other lizard diets (e.g., *Aspidoscelis tigris*, Best and Gennaro 1985; *Ameivula nativo*, Menezes et al. 2008). Despite their abundance, insect eggs contributed minimally to dietary volume and frequency, likely due to their small size and limited intake. Interestingly, only a few adult lizards (seven females and four males) consumed insect eggs, primarily during the reproductive peak in the second year. This suggests that insect eggs, which are rich in lipids and other nutrients (Wheeler 2003), may serve as a supplementary resource during periods of high energy demand. Their low dietary frequency, however, indicates opportunistic feeding when these eggs are temporarily abundant.

Prey consumption by *C. vacariensis* differed significantly from invertebrate availability across all seasons during the first year, indicating selective feeding. Trophic niche breadth was greatest in summer and paralleled seasonal prey availability in all climate seasons, a pattern that contrasts with the predictions of Optimal Foraging Theory (MacArthur and Pianka 1966), which anticipates dietary generalization when resources are abundant and specialization when they are scarce. Instead, *C. vacariensis* maintained selectivity year-round, broadening its diet when prey was abundant and narrowing it as resources declined. This deviation may stem from microhabitat use and foraging mode: unlike other teiids that forage extensively in open areas (e.g., *Ameivula nativo*, Menezes et al. 2008; *A. ocellifera*, Sales et al. 2012), *C. vacariensis* spends most of its activity under rocks or in burrows (Caruccio et al. 2010), where individuals were often found with dominant prey items (Laura Verrastro and Martin Schossler, pers. comm.). Such plasticity in foraging strategy may enhance persistence in the temperate grasslands of the Araucaria Plateau.

Interestingly, Collembola were the most abundant arthropods in the habitat during winter and spring and the second most abundant group in summer and autumn during the first year, but no *C. vacariensis* individuals consumed Collembola throughout the study. This avoidance may be attributed to chemical defenses of Collembola, which deter predators (Messer et al. 2000; Möllerke and Schulz 2025). Conversely, Orthoptera, a medium-to-large prey item, were consumed disproportionately to their low environmental abundance, suggesting that prey size influences dietary selection more than abundance. Therefore, our findings also suggest potential individual specialization in diet (ISD), where individual diets form subsets of the overall niche of the population (Svanbäck and Bolnick 2008). ISD has been observed in other taxa, including *Tropidurus* spp., *Cnemidophorus* spp. (Costa et al. 2008), the Neotropical Ameiva (*Ameiva* ameiva; Costa et al. 2008; Sales et al. 2011), and *Ameivula ocellifera* (Zanchi-Silva et al. 2020), but remains understudied in *C. vacariensis*. Further research is needed to confirm ISD in this species and to explore its underlying mechanisms, whether related to prey size or other factors.

Contomastix vacariensis showed no significant differences in diet composition between sexes, age classes, seasons, or years, indicating a stable trophic structure maintained across both demographic and temporal scales. The absence of sexual and ontogenetic variation in teiid diets is often associated with extensive consumption of aggregated prey, such as termites and insect larvae, which tends to minimize dietary divergence, as seen in *Glaucomastix littoralis* (Teixeira-Filho et al. 2003; Menezes et al. 2006), *Teius oculatus* (Capellari et al. 2007), *Ameivula nativo* (Menezes et al. 2008), and *A. ocellifera* (Menezes et al. 2011; Sales et al. 2012). These prey types were rarely consumed in *C. vacariensis*. Even the marked ingestion of insect eggs by a few adult individuals during the second year, which represented approximately 80% and 25% of the total diet of females and males, respectively, was insufficient to produce significant sexual or ontogenetic differences.

Seasonal stability was also evident throughout our 2-y study. This contrasts with the marked shifts reported for the Lagartixa-da-Praia (*Liolaemus occipitalis*) in coastal sand dunes of southern Brazil (Verrastro and Ely 2015). While *L. occipitalis* exhibited dietary differences across most seasons, *C. vacariensis* maintained a relatively consistent prey composition year-round in both years. The absence of seasonal variation suggests that prey consumption in *C. vacariensis* is less influenced by temporal changes in factors such as rainfall, as has been found for *Aspidoscelis tigris* (Best and Gennaro 1985), the Pondichéry Fan Throated Lizard (*Sitana ponticeriana*; Pal et al. 2007), and *Aspidoscelis lineatissima* (Rodríguez and Casas-Andreu 2011), or for temperature (e.g., *L. occipitalis*, Verrastro and Ely 2015). The spring peak in egg consumption during the second year was driven by four individuals that consumed 339 eggs, which also was insufficient to generate a broader seasonal dietary pattern.

Although multivariate diet composition did not vary between years, univariate analyses revealed significant interannual differences in NP and LL. These changes may reflect annual fluctuations in prey abundance, prey size structure in the environment, or behavioral shifts in prey capture strategies, without altering the overall taxonomic profile of the diet. In particular, the higher NP and LL values observed in the second year suggest that lizards may have increased both prey intake and maximum prey size, potentially in response to more favorable foraging conditions or altered prey communities.

In *C. vacariensis*, individuals with larger SVL consumed longer and more voluminous prey (LL, ML, and MV), but not more items (NP), indicating that body size limits prey dimensions rather than quantity. MO, despite its strong correlation with SVL, had no independent effect on prey size, suggesting that SVL reflects traits such as bite force and jaw leverage that define the upper limit of prey dimensions (Verwaijen et al. 2002; Herrel and Holanova 2008). This link between predator size and prey dimensions is common among generalist lizards (Vitt and Pianka 2007) and appears in related taxa. For instance, *C. vacariensis* resembles *Teius oculatus*, which also showed a positive predator-prey size relationship (Capellari et al. 2007) but, unlike most teiids (e.g., *Glaucomastix littoralis*, Teixeira-Filho et al. 2003; Menezes et al. 2006; *Ameivula nativo*, Menezes et al. 2008), did not focus on small prey. Similar patterns occur in *A. nativo* (Menezes et al. 2008) and *A. ocellifera* (Sales et al. 2012), where larger individuals consumed more voluminous prey. Yet *C. vacariensis* differs in showing marked variation in prey size linked to body size, likely reflecting the advantages of larger morphology rather than MO alone.

Despite these size-related effects, no sexual differences were detected in prey quantity or dimensions, with both sexes exploiting a wide range of prey sizes. This agrees with patterns reported for other teiids (e.g., *Glaucomastix littoralis*, Menezes et al. 2006; *Teius oculatus*, Capellari et al. 2007; *Ameivula ocellifera*, Sales et al. 2012), where sexual variation in diet is often absent. In *C. vacariensis*, the lack of sexual and ontogenetic divergence may reflect the fact that both sexes and both age classes consumed proportionally larger prey in the second year, coinciding with the observed increase in LL values across all groups. Even in *A. ocellifera*, where head length is sexually dimorphic, diets remain similar between sexes, dominated by small prey such as termites (Sales et al. 2012). Thus, although *C. vacariensis* consumes a broader range of prey sizes, the proportional increase in larger prey across demographic groups may homogenize dietary metrics between sexes and age classes.

In conclusion, *Contomastix vacariensis* primarily feeds on insect eggs, Araneae, and Orthoptera in the high-elevation grasslands of the Araucaria Plateau. Prey consumption differed from environmental availability during the first year, and prey size and volume were positively associated with lizard body size, while MO had no independent effect. Interannual differences were detected for NP and LL, with higher values in the second year. The proportional increase in larger prey across both sexes and age classes in that year likely reduced potential sexual or ontogenetic differences, resulting in stable prey dimensions and composition across demographic groups. *Contomastix vacariensis* is a generalist consumer with selective use of available prey, maintaining a stable trophic structure across demographic and temporal scales, and with prey dimensions strongly constrained by body size.

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APPENDIX

Appendix Table 1. Comparison of invertebrates collected in the habitat with the diet of Lagarto-Pintado (*Contomastix vacariensis*) across seasons in the grasslands of the Araucaria Plateau, Vacaria, southern Brazil, between September 2004 and August 2005. Values for the number of invertebrates in the habitat and prey items in the diet are expressed as percentages. The abbreviation UA = unidentified arthropods.

	Winter		Spring		Summer		Autumn	
Items	Habitat	Diet	Habitat	Diet	Habitat	Diet	Habitat	Diet
	N (%)	N (%)	N (%)	N (%)	N (%)	N (%)	N (%)	N (%)
Annelida								
Oligochaeta	–	–	15 (0.14)	–	26 (0.18)	–	2 (0.02)	–
Arachnida								
Acari	112 (1.97)	1 (1.47)	345 (3.32)	–	419 (2.91)	–	147 (1.59)	–
Aranae	437 (7.69)	10 (14.71)	526 (5.06)	22 (40.74)	1663 (11.53)	16 (34.04)	570 (6.17)	2 (5.00)
Opilionida	48 (0.84)	1 (1.47)	82 (0.79)	–	65 (0.45)	–	33 (0.36)	–
Pseudoscorpiones	–	–	12 (0.12)	–	–	–	–	–
Scorpiones	2 (0.04)	4 (5.88)	7 (0.07)	2 (3.70)	51 (0.35)	–	19 (0.21)	1 (2.50)
Crustacea								
Isopoda	7 (0.12)	–	22 (0.21)	–	9 (0.06)	–	2 (0.02)	–
Hexapoda								
Blattodea	7 (0.12)	3 (4.41)	41 (0.39)	3 (5.56)	77 (0.53)	7 (14.89)	56 (0.61)	3 (7.50)
Coleoptera	211 (3.71)	1 (1.47)	761 (7.33)	7 (12.96)	842 (5.84)	–	395 (4.27)	–
Collembola	2364 (41.58)	–	4049 (38.97)	–	3898 (27.03)	–	3435 (37.16)	–
Dermaptera	6 (0.11)	–	206 (1.98)	–	19 (0.13)	–	46 (0.50)	–
Diptera	523 (9.20)	–	781 (7.52)	1 (1.85)	573 (3.97)	–	474 (5.13)	–
Hemiptera	105 (1.85)	–	233 (2.24)	–	319 (2.21)	–	172 (1.86)	2 (5.00)
Hymenoptera	1596 (28.07)	32 (47.06)	2903 (27.94)	4 (7.41)	5935 (41.16)	2 (4.26)	3587 (38.81)	4 (10.00)
Isoptera	3 (0.05)	–	45 (0.43)	–	22 (0.15)	–	12 (0.13)	–
Lepidoptera	3 (0.05)	–	3 (0.03)	–	2 (0.01)	–	4 (0.04)	–
Orthoptera	49 (0.86)	13 (19.12)	109 (1.05)	10 (18.52)	325 (2.25)	18 (38.30)	219 (2.37)	22 (55.00)
Psocoptera	10 (0.18)	–	3 (0.03)	–	7 (0.05)	–	1 (0.01)	–

Appendix Table 1, Continued

Items	Winter		Spring		Summer		Autumn	
	Habitat	Diet	Habitat	Diet	Habitat	Diet	Habitat	Diet
	N (%)	N (%)	N (%)	N (%)	N (%)	N (%)	N (%)	N (%)
Trichoptera	–	–	–	–	–	–	5 (0.05)	–
Thysanura	7 (0.12)	–	29 (0.28)	–	71 (0.49)	–	27 (0.29)	–
Thysanoptera	1 (0.02)	–	–	–	–	–	–	–
Coleoptera larvae	16 (0.28)	1 (1.47)	65 (0.63)	–	71 (0.49)	–	18 (0.19)	–
Diptera larvae	3 (0.05)	–	–	–	–	–	–	–
Lepidoptera larvae	125 (2.20)	–	8 (0.08)	–	18 (0.12)	–	10 (0.11)	–
Insect ootheca	–	1 (1.47)	–	–	–	–	–	–
Insect pupae	–	–	–	1 (1.85)	–	–	–	–
Mollusca								
Gastropoda	–	–	–	1 (1.85)	–	–	–	–
Myriapoda								
Chilopoda	–	–	7 (0.07)	–	7 (0.05)	–	5 (0.05)	–
Diplopoda	50 (0.88)	–	137 (1.32)	–	1 (0.01)	–	4 (0.04)	–
Others								
Mineral material	–	–	–	–	–	–	–	4 (10.00)
Plant material	–	–	–	3 (5.56)	–	–	–	–
UA	–	1 (1.47)	–	–	–	4 (8.51)	–	2 (5.00)
∑	5685 (100)	68 (100)	10389 (100)	54 (100)	14420 (100)	47 (100)	9243 (100)	40 (100)

Appendix Table 2. Diet of Lagarto-Pintado (*Contomastix vacariensis*) across climatic seasons in the grasslands of the Araucaria Plateau, Vacaria, southern Brazil, based on 175 specimens collected between September 2004 and August 2006. Values for number of prey items (N), volume (V), frequency of occurrence (F) are expressed as percentages. Importance value index (IVI) represents the mean of the percentage values of N, V, and F. Abbreviation: UA = unidentified arthropods.

	Winter (n =37)				Spring (n = 55)				Summer (n = 42)				Autumn (n = 41)			
Prey Items	N (%)	V (%)	F (%)	IVI	N (%)	V (%)	F (%)	IVI	N (%)	V (%)	F (%)	IVI	N (%)	V (%)	F (%)	IVI
Mollusca																
Gastropoda	–	–	–	–	0.20	0.06	1.82	0.69	–	–	–	–	–	–	–	–
Arachnida																
Acari	0.86	0.00	2.70	1.19	–	–	–	–	–	–	–	–	–	–	–	–
Araneae	25.00	17.16	43.24	28.47	11.63	24.65	63.64	33.31	19.64	15.96	45.24	26.95	12.50	8.70	26.83	16.01
Scorpiones	4.31	22.05	13.51	13.29	1.22	4.14	9.09	4.82	0.89	1.64	2.38	1.64	2.50	4.54	7.32	4.79
Opilionida	0.86	0.65	2.70	1.40	–	–	–	–	–	–	–	–	–	–	–	–
Hexapoda																
Blattodea	4.31	29.39	13.51	15.74	3.67	49.51	21.82	25.00	9.82	30.33	26.19	22.11	5.00	20.33	9.76	11.70
Coleoptera	0.86	0.10	2.70	1.22	1.63	1.45	10.91	4.66	–	–	–	–	–	–	–	–
Diptera	–	–	–	–	0.41	1.36	3.64	1.80	–	–	–	–	0.83	0.02	2.44	1.10
Hemiptera	–	–	–	–	0.20	0.01	1.82	0.68	0.89	4.88	2.38	2.72	2.50	6.62	7.32	5.48
Hymenoptera	31.90	1.64	29.73	21.09	2.86	1.76	10.91	5.18	7.14	0.78	9.52	5.82	3.33	0.29	9.76	4.46
Isoptera	–	–	–	–	–	–	–	–	–	–	–	–	2.50	0.07	2.44	1.67
Mantodea	–	–	–	–	0.20	0.28	1.82	0.77	–	–	–	–	0.83	0.34	2.44	1.20
Orthoptera	17.24	18.06	40.54	25.28	3.06	3.89	21.82	9.59	19.64	32.49	38.10	30.08	34.17	39.19	46.34	39.90
Insect egg	1.72	0.06	2.70	1.50	69.18	0.10	7.27	25.52	26.79	0.05	2.38	9.74	20.83	7.05	12.20	13.36
Insect larvae	0.86	2.64	2.70	2.07	–	–	–	–	–	–	–	–	2.50	0.77	7.32	3.53
Coleoptera larvae	0.86	0.49	2.70	1.35	–	–	–	–	–	–	–	–	0.83	1.87	2.44	1.71
Lepidoptera larvae	–	–	–	–	–	–	–	–	1.79	5.05	2.38	3.07	–	–	–	–
Insect ootheca	2.59	5.30	8.11	5.33	1.22	8.62	5.45	5.10	1.79	5.49	4.76	4.01	–	–	–	–
Insect pupae	–	–	–	–	0.20	2.27	1.82	1.43	–	–	–	–	–	–	–	–
Others																
Mineral material	0.86	1.62	2.70	1.73	0.82	0.31	7.27	2.80	5.36	1.53	14.29	7.06	7.50	4.93	21.95	11.46
Plant material	2.59	0.19	8.11	3.63	1.84	1.15	16.36	6.45	0.89	0.08	2.38	1.12	0.83	0.12	2.44	1.13
UA	5.17	0.65	16.22	7.35	1.63	0.44	14.55	5.54	5.36	1.71	14.29	7.12	3.33	5.15	9.76	6.08
Sum	100	100	–	–	100	100	–	–	100	100	–	–	100	100	–	–

Appendix Table 3. List of voucher specimens of Lagarto-Pintado (*Contomastix vacariensis*) deposited in the Scientific Collection of Herpetology of the Department of Zoology of the Universidade Federal do Rio Grande do Sul (UFRGS).

First Year (between September 2004 and August 2005)												Second Year (between September 2005 and August 2006)											
Winter			Spring			Summer			Autumn			Winter			Spring			Summer			Autumn		
3696	3697	3698	3746	3747	3748	3788	3789	3790	3868	3869	3870	3954	3955	3956	3968	3969	3970	4033	4034	4035	4049	4050	4051
3699	3700	3701	3749	3750	3751	3791	3792	3793	3871	3872	3873	3957	3958	3959	3971	3972	3974	4036	4037	4038	4052	4053	4054
3702	3703	3704	3752	3753	3754	3794	3795	3796	3874	3875	3876	3960	3961	3962	3975	3976	3977	4039	4040	4041	4055	4056	4128
3705	3924	3925	3755	3757	3758	3814	3815	3816	3877	3878	3882	3963	3964	3965	3978	3979	3980	4042	4043	4044	4129	4130	4131
3926	3927	3928	3759	3760	3761	3817	3818	3819	3883	3885	3886	4216	4217	4218	4000	4001	4002	4045	4046	4047	4132	4133	4135
3929	3930	3931	3763	3764	3765	3820	3821	3822	3887	3888	3889	4219	4220	4242	4003	4004	4005	4048	–	–	4136	4137	4138
3932	3933	3934	3766	3767	3768	3823	3824	3825	3890	3891	3892	4243	4244	4245	4006	4007	4008	–	–	–	4139	4140	4141
3935	3936	3939	3771	3772	3773	3847	3848	3849	3893	3894	3908	4246	–	–	4009	4010	4022	–	–	–	4142	4143	4144
3940	3941	3942	3774	3775	3776	3850	3851	3852	3909	3910	3911	–	–	–	4023	4024	4025	–	–	–	4149	4150	4151
3943	3944	3945	3777	3778	3779	3853	3854	3855	3912	3913	3914	–	–	–	4026	4027	4028	–	–	–	4152	4153	4154
3946	3947	3948	3780	–	–	3856	–	–	3915	3916	–	–	–	–	4029	4030	4031	–	–	–	4155	–	–
3949	3950	3951	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–