Habitat choice shaping nestling growth

An exploratory study on environmental factors affecting growth in a wild insectivorous passerine

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The effect of habitat choice is only as great as the habitat's effect on its inhabitants' fitness. After all, if there were no fitness consequences, habitat choice would not matter. Previously, studies have often used singular environmental factors as proxies for the effects of habitats on organism fitness, potentially overlooking the true mechanisms behind habitat selection patterns. Here, we measured several environmental habitat factors and tested their (interacting) effects on the growth of the offspring of the thorn-tailed rayadito (*Aphrastura spinicauda*), a widespread South American nestbox inhabiting passerine. We found that specific habitat types are associated with differences in nestling growth, as the habitat with the densest vegetation was found to have lower offspring growth. Across several analyses of different growth measures, vegetation measures such as foliage coverage, diameter breast height, and the number of deciduous trees were generally also found to positively affect nestling growth. This was not found for insect abundance. Despite this, together with existing literature, these findings point towards vegetation being a good proxy for habitat choice for insectivorous passerines, as vegetation is often correlated with food abundance and can explain this distribution due to its importance for insect ecology. As such, research focussed on the habitats of insectivorous passerines could benefit from focussing on the vegetation aspects of habitats as it can work as an indirect measure for food abundance.

Keywords: habitat quality, environmental effect, vegetation, foliage, mid-successional forest, thorn-tailed rayadito, Aphrastura spinicauda

1. Introduction

The field of ecology as a whole is built upon the interactions of organisms with each other and their biophysical environment, be it biotic or abiotic. The environment which affects organisms the most is of course their habitat. As such, interactions between organisms and their habitats are well studied, but arguably not well understood. This is mainly because habitat quality can be quantified in many ways. Afterall, what defines habitat quality? Most argue that the factor that inhibits organisms' fitness the most is often the most defining (Tremblay et al. 2005). This is especially apparent in many birds such as the blue tit (Cvanistes caeruleus) and the great tit (Parus major) who experience significant spatial and temporal variation in food abundance (Tremblay et al. 2005). This is mainly because their most prominent food source, caterpillars, are only abundant for a short seasonal peak in any habitat (Perrins 1991, Blondel et al. 1991, Banbura et al. 1999). Thus, birds will have to adapt their own reproduction cycle to these seasonal peaks in their habitats, causing those that are unable to do this to have a decreased fitness (Tremblay et al. 2005). However, the overall abundance of these caterpillars is known to differ tremendously between habitats (Tremblay et al. 2003), resulting in food abundance being the limiting factor for a habitat and thus a good quantitative measure (Tremblay et al. 2005).

Nevertheless, a quantitative habitat measure is only as good as its effect it has on its inhabitants. In the case of food abundance, its effects are quite broad (Tremblay et al. 2005). For tits, it has been found that food abundance affects traits related to clutch size, laying timing, nestling development, and nestling growth (Perrins 1970, Nour et al. 1998, Tremblay et al. 2003). This factor is thus very present in habitats and affects the organisms quite heavily (Tremblay et al. 2005). However, habitats might differ significantly in certain factors, such as altitude, without them necessarily affecting the inhabiting organisms (overlooking extreme differences; (Moreng 1983). Thus, the best measures for habitats are those that are both present in habitats and affect the inhabiting organisms in some way that affects their fitness. For example, food availability is a factor that affects egg- and offspring size as well having significant spatial and temporal variation, meaning its effects can be tested for (Richner 1989, Smith and Bruun 1998, Tremblay et al. 2005). Early life history fitness can also be affected by provisioning behaviour and nestling feeding rates, which in turn can often be affected by weather, temperature, food availability, and offspring diet (Cullen et al. 1996, Dawson and Bortolotti 2000, Pinaud et al. 2005, Wilkin et al. 2009).

Of course, all these habitat components are usually tested separately without an eye for potential interactions between these factors. Most studies were conducted with a specific habitat measure in mind such as food abundance, but rarely are these studies ever exploratory to discover the interplay between habitat components and see which are the most significant for organism fitness. By looking at multiple variables as well as their interactions, the chance to uncover the underlying mechanisms behind habitat selection are much stronger.

In this study, we aimed to discover what environmental factors within the habitat of the thorn-tailed rayadito (Aphrastura spinicauda) affect their fitness, quantified through the growth of their offspring. Reproductive success is often used as a measure for fitness and, although indirectly, the growth of the offspring can be seen as measure of reproductive success and thus a good fitness measure (Lloyd and Martin 2004). This study was part of a larger scale study aiming to discover the physical differences in the thorn-tailed rayadito between two climatic extremes situated in Chile. These two climatic extremes are the northern province of Villarrica and the southern island of Navarino. These sites differ tremendously in climate, as Villarica has a temperate Mediterranean climate, and Navarino has a sub-Antarctic climate. This allows for a comparative study like this for the effects of different environmental factors. These sites had habitat differences within them as well, allowing for testing of the factors themselves rather than it just being an effect of the climatic extremes.

These tested habitat differences were based upon previous research and existing literature. Firstly, an overall habitat effect would be required for a more in-depth analysis on specific environmental factors within habitats. Habitat differences were furthermore found to affect offspring growth (Richner 1989, Smith and Bruun 1998). As for the specific environmental factors within the habitats, we measured several vegetation based measures, as vegetation has been found to affect offspring growth in the past (Erikstad 1985, Kim and Monaghan 2005). Vegetation can also serve as a indicator for food abundance, as prey item density is often determined by several vegetation measures such as foliage density and the presence of certain tree species (Moorcroft et al. 2002). Food availability has of course also been found to affect nestling growth and was thus also taken into consideration (McKinnon et al. 2012). The same goes for effects such as clutch size (Groves 1984), environmental temperature (Mickelberry et al. 1966), and precipitation and weather effects (Christensen-Dalsgaard et al. 2018).

For this research, we asked the question: "How do biotic- and abiotic components of an ecosystem and their interactions affect the offspring growth and fledging measurements in two climatically different populations in the thorn-tailed rayadito?". We predicted that food abundance and vegetation measures are associated with offspring growth the most. The latter in particular for its correlation with the former (Moorcroft et al. 2002).

2. Methods

2.1 Study sites

This study was conducted in the field seasons (September – January) of 2018/2019 and 2019/2020 on a wild nestbox population of the thorntailed rayadito. The study took place in two climatic extremes in Chile, South America. One site is in the north in the province of Villarrica, Araucanía (~ -39.282761, -72.228182), and the other site is located in the south on the island Navarino in the town Puerto Williams, Cabo de Hornos, Magallanes y la Antártica Chilena (~ -54.935245, -67.605919 figure 1). The northern site has 200 nestboxes and the southern site has 220. Although these are two different locations, it is one rayadito population with lots of gene flow, but will henceforth be referred to as 'sites' for simplicity. In conjunction with the Universidad de Chile and Pontificia Universidad Católica de Chile, we were allowed to use this pre-existing infrastructure of nestboxes that has been in place in Villarrica since 2007, and in Navarino since 2001.



2.2 Field data

The thorn-tailed rayadito lays eggs with a one-day gap, meaning once the laying dates were known, it was easy to predict when eggs would be laid. As such, all nestboxes were checked for activity every four days. If indications of nest building were found inside the boxes, they were checked every two days. If eggs were found, they were marked, and we would return the next day to determine the laying order of the nest. All eggs were weighed and measured in length and width. If the last egg in the clutch was laid, we called the clutch completed at clutch completion day zero (or CC0). From CC12 onwards, we checked the nest daily for the eggs to hatch. Once hatched (D0), the nestlings were weighed and marked for individual identification by clipping their toenails. Once the oldest nestling was four days old (D4), we would return to the nest and weigh the nestlings again as well as measure the length of their culmen in millimetres. The nestlings were afterwards measured again on D8, D12, and D16. From day eight onwards, the nestlings' tarsus length and wing length were also measured aside from the already being measured weight and culmen length. The nestlings were also ringed on day eight for more reliable identification purposes. All field measures in relation to the physiology of the thorn-tailed rayadito were based upon earlier conducted research (Moreno et al. 2005, Altamirano 2014).

2.3 Environmental data

Near the end of the field season, when all trees are in full bloom, certain environmental factors for determining habitat quality were measured based on literature. This was conducted in an 11,2-meter radius around occupied nestboxes to standardize between nestboxes, as based on previous research (Altamirano 2014). These factors were tree numbers, tree species, tree diameter, foliage coverage at different heights, and habitat type. The latter foliage coverage was measured from 0-3 metres, 3-5 metres, and 5 > metres. This was measured by estimating the coverage in percentage at those given heights per nestbox. The tree diameter (diameter breast height, or DBH) was measured at observer chest height with a measuring tape held around the tree. This was only done for trees with a higher diameter than 12,5 cm in accordance to previous research (Altamirano 2014). The tree species were determined, counted, and subsequently divided between being deciduous or evergreen, as certain prey items (such as caterpillars) prefer deciduous trees over evergreen trees.

The last measured environmental factor was the habitat type which the nestboxes occupy. This was done by categorization of said habitats. In total we quantified five different habitat types: (1) old growth forest, (2) mid successional forest with understorey, (3) mid successional forest without understorey, (4) early successional forest, and (5) mixed shrubland. These types were determined based on the age of the trees, foliage decay, and the presence of foliage at certain levels. For example, the old growth forest consisted of old trees and lots of decay, the mid successional forest with understorey was a healthy forest with a lot of foliage coverage, the early successional forest is not more than 10 metres high, and the mixed shrubland featured many thick shrubs. Although mostly, the habitat types were determined by pre-existing knowledge of which habitats the nestboxes were placed in conducted by those who set up the nestbox infrastructure.

Insect counts were done every 8 days per site as a measure of food availability using the 'beat-sheet' method (Wade et al. 2006). In short, a small tarp (80x80x80 cm) was held underneath tree branches which were hit with a stick 10 times to make insects drop from the tree onto the tarp. This method would be conducted on four random trees per site (Villarica and Navarino). The insect totals would be counted and averaged over these trees to obtain the insect abundance per site. Note again that this measure was conducted per site, not per nestbox like most other environmental variables.

Average air temperature and accumulated precipitation data were collected from weather stations close to the sites. The data from the northern site was collected from the San Enrique weather station in Pucón, and the data from the southern site was collected from the Puerto Williams weather station. Datapoints were taken for the average temperature and accumulated precipitation per week, allowing to take variations in these environmental variables into account, while not either having singular extremes stand out in the data, or eliminating this variance by averaging over longer time periods.

2.4 Statistical analyses

Analyses were done in R 3.5.3 (R Core Team 2018) using RStudio 1.1.456 (RStudio Team 2015). Two separate groups of analyses were conducted on the growth rates of the nestlings and on the fitness measures before fledging. The fitness measures used for these analyses were body mass, tarsus length, culmen length, and the residuals of the regression between body mass and tarsus length. The latter was included to estimate a general combined condition measure, rather than looking at just a singular component of nestling growth. Henceforth it will be referred to as body condition index for simplicity. For both analyses, a principal component analysis (PCA) was conducted to view data variance, and a generalized linear mixed model (glmm) was constructed to analyse the data for significant effects on nestling growth/fledging measures.

For further analysis, a food index was calculated, and variable environmental data was adjusted to the appropriate timespan. Regarding the former, the food index was calculated by multiplying all insect abundance measures with 0-3 metre foliage coverage. This was done as insect counts were not conducted per nestbox, but per site. Foliage coverage was chosen here as the insect abundance counts were based on the insects present on the 0-3 metre foliage. Furthermore, insect abundance and foliage coverage is often correlated (Gunnarsson 1990). This results in a nestbox-specific index for food abundance. Through this calculation, this index considers a seasonal factor, as through the beat-sheet method it can detect when in the food peak the birds are breeding. It also includes a spatial component through the vegetation in that specific habitat, as well as a broader scale spatial component by the foliage providing information on the climate. Aside from that, it is important to note that air temperature, precipitation, food index, and insect abundance were averaged over certain time periods depending on the analysis. In the case of the growth analyses, these environmental variables would be averaged for the entire period of the nestling's growth, which is a three-week period. Henceforth these environmental are described as average air temperature, average precipitation, average food abundance, and average food index. For the fledging analysis on the other hand, only the measure of one week of these environmental variables was used. This was done to properly address the effect these environmental variables might have on the growth/fledging measures. After all, one measure of these variables taken at one point in time most likely does not predict the effect it has on growth properly. All other environmental factors were static across the nestlings' growth periods and were thus not averaged out over the nestlings' growth periods.

Graphs featured in this report were constructed using the ggplot2 package in R (Wickham 2016).

2.4.1 Analysis procedures

For each analysis, the fixed predictor variables were foliage coverage at separate heights (0-3m, 3-5m, 5m>), (average) insect abundance, (average) air temperature, (average) accumulated precipitation, (average) food index, site (Villarrica or Navarino), habitat type, clutch size, total number of trees (evergreen and deciduous), and average chest-height diameter of these trees. The indicated predictor variables would only be averaged in the case of the growth analyses, as mentioned before. The random predictor variables were nestbox and observer to account for variances these might have caused. The model also featured interactions between 0-3 metre foliage coverage and 5> metre foliage coverage, and between 3-5 metre foliage coverage and 5> metre foliage often affects the presence of high foliage and vice-versa (Bakker et al. 2004). Following this full model, chi-square ANOVA's were conducted to determine which predictor variables significantly affected the respective growth measure. The most nonsignificant predictor variables were step-wise dropped from the model according to Ockham's razor to end up with a minimum adequate model (MAM henceforth) with only variables that significantly affect the respective growth measure (Schaffer 2015). AIC values were also considered whenever variables were removed. However, each added predictor variables explains a fraction of the variance in the data. So while the deletion of insignificant predictor variables might result in a higher AIC value compared to the original model (Harrison et al. 2018), this method was still preferred here as it does reveal the environmental variables that affect the respective growth/fledging measures the most, which is what we wanted to uncover. It is furthermore worth noting that I chose to remove insignificant (singular) random predictor variables as I was in favour of running high-power studies as suggested by Bates et al. (Bates et al. 2015). If this were needed, the generalized linear mixed model would be converted into a general linear model. Whether glmm or glm, the distribution family used in the model was the gaussian distribution.

Lastly, a post-hoc analysis was conducted to determine significant differences within a group, such as the different categorical habitat types in the habitat type variable. This was done with both a pairwise t-test and Tukey's 'Honest Significant Difference' method. Post-hoc p-values noted in this paper were derived from the latter.

2.4.2 Nestling growth analysis

For the nestling growth measures, different growth models were applied to view the best fit (using adjusted R-squared). Linear growth models, parametric nonlinear growth models, and Gompertz growth models were employed and their fit (R-squared) compared. The Gompertz model had the highest fit and thus were used for further analysis. For all nestlings, a Gompertz growth model was fitted to the respective data and an average growth or increase value was extracted from this model to be used in analysis, henceforth simply referred to as 'growth'. For mass and culmen length, data gathered at D0, D4, D8, D12, and D16 was used. For tarsus length, only data from D8, D12, and D16 was used, as tarsus length was not measured earlier in nestling development.

The generalized linear mixed model used body mass growth, tarsus length growth, culmen length growth, and the residuals of the regression between body mass growth and tarsus length growth (body condition index growth) as response variables. The fixed predictor variables insect abundance, air temperature, accumulated precipitation, and food index were averaged over the three-week period of the nestlings' growth.

2.4.3 Nestling fledge measure analysis

The fitness measures near fledging age were tested whether these were associated with several environmental factors. After all, individuals might differ in growth rate, but could still end up with the same fitness measures near fledging. The thorn-tailed rayadito fledged between 18-22 days of age (Altamirano 2014). However, because we did not want to risk premature fledging from the nestlings, we chose to measure them at day sixteen (D16) when they're not yet capable of doing this while still getting measurements representative of those near the fledging stage.

The generalized linear mixed model used D16 mass, D16 tarsus length, D16 culmen length, and the residuals of the regression between D16 body mass and D16 tarsus length (fledging body condition index) as response variables.

3. Results

As multiple analyses were conducted depending on the growth measures, the fledging measures, and the separate fitness measures (body mass, tarsus length, and culmen length), the results section is split between these analyses. First the four analyses on the separate growth rates will be shown, followed by the four fledging measures analyses. All significant findings are mentioned here, but not always shown. Results not shown here can be found in the appendix at the end of the article.

In total there were 46 nests with nestlings that reached day 16 and 192 nestlings that reached day 16.

3.1 Offspring growth

3.1.1 Offspring body mass growth

Habitat type was found to significantly affect body mass growth (p=0.044; figure 2) together with air temperature and site (p=0.035 and p=0.011, respectively; figure 3 and 4).



Conducting a post-hoc analysis on the different habitat types reveals that the underlying habitats do not differ significantly from one another.



Figure 3. Effect of site on the body mass growth in the thorn-tailed rayadito offspring

Different sites can be seen on the x-axis, as well as them being explained in the top-right legend. The yaxis displays the body mass growth The numbers in the boxplots are the sample sizes per site.

16 Air temperature (degrees Celsius) Relation 4 Figure between average aiı temperature and body mass growth of the thorntailed rayadito

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The x-axis displays the air temperature in degrees Celsius. The y-axis displays the body mass growth of the thorn-tailed rayadito offspring

As can be seen in figure 3, the body mass growth of nestlings in Navarino is significantly higher than those in Villarica. Figure 4 showcases that nestlings in higher air temperature have a significantly lower body mass growth than nestlings in lower air temperatures. However, when comparing these two figures together, it becomes evident that these are the same data points.

3.1.2 Offspring tarsus length growth

Construction of the MAM leaves the following variables that significantly affect the tarsus length growth: habitat type (p=0.007; figure 5), average chest-height tree diameter (p=0.027; appendix 7.1), and the interactions between foliage coverage 5>m and foliage coverage 0-3m (p=0.003; figure 6). Low foliage coverage (0-3m) itself was also found to significantly affect the tarsus length growth (p=0.043).



A post-hoc analysis shows that within the different habitat types, nestlings in the mixed shrubland were found to have a significantly higher tarsus length growth slope than nestlings in the early successional forest (p=0.032) and showed a trend for nestlings having a higher growth slope than those in the mid successional forest with no understorey (p=0.081). Furthermore, nestlings in the mid successional forest with understorey were found to have a significantly higher tarsus length growth slope than those in the early successional forest (p=0.023).



Figure 6. Effect of interaction between foliaae coveraae 0-3m and foliage coverage 5m> on the tarsus length growth.

The tarsus length growth slope is displayed on the x-axis and the foliage coverage 5m> and 0-3m are seen on the left and right y-axis respectively. The legend in the top right corner explains which colours is representative of which graph.

As seen in figure 6, foliage coverage 0-3m and foliage coverage 5m> interact with one another such that when they both increase, the tarsus length growth slope also increases significantly (p=0.003 **). Foliage coverage 0-3m itself was also found to significantly affect the tarsus length growth slope (p=0.02 *).

3.1.3 Offspring culmen length growth

Culmen length growth was found to be significantly affected by site (p=0.045; figure 7), and habitat type showed a trend (p=0.054; figure 8) after all other variables were stepwise removed from the model. Note that foliage coverage 5>m and average insect count themselves separately were not found to significantly affect the culmen length growth.



Figure 7. Effect of site on the culmen length growth of the rayadito offspring.

The different sites are seen on the x-axis as well as being explained in the top-right legend. On the yaxis is the growth of the culmen lenath. The numbers in the boxplots are the sample sizes per habitat.

respectively).

As seen in figure 7, culmen length growth was found to be significantly higher for nestlings in Navarino than for nestlings in Villarrica (p=0.045).



A post-hoc analysis showed that the culmen length growth slope of nestlings in the mixed shrubland habitat was significantly higher than that of the nestlings in the mid successional forest with understorey (p=0.029).

3.1.4 Offspring body condition index growth

Here it was found that body condition index growth is significantly affected by habitat type (p<0.0001; figure 9). It is furthermore significantly positively correlated with 0-3 metre foliage coverage (p=0.005; figure 10), accumulated precipitation (p=0.039; appendix 7.2), and significantly negatively correlated with breast height tree diameter (p=0.018; appendix 7.3).



Following these findings, a post-hoc analysis showed that nestlings in the mid-successional forest with understorey had a significantly higher body condition index growth than nestlings in both the mid successional forest without understorey and the early successional



Figure 10. Relation between 0-3 metre foliage coverage and the residuals of the regression between body mass growth and tarsus length growth (body condition index growth).

The x-axis displays 0-3 metre foliage coverage in percentage and the y-axis shows the body condition index growth.

3.2 Offspring fledging measure

3.2.1 Offspring fledging body mass

Habitat type was found to significantly affect the day 16 body mass after constructing the MAM for this fledging measure (p=0.0008; figure 11).

forest (p=0.0005 and p=0.0004, respectively). Nestlings in the mixed

shrubland were also found to have significantly higher body condition

index growth than those in the mid successional forest without

understorey and the early successional forest (p=0.025 and p=0.046,



Habitat type

A subsequent post-hoc analysis revealed that the day 16 body mass of the nestlings in the mid successional forest with understorey was significantly lower than that of nestlings in the mid successional forest with no understorey, the early successional forest, and the mixed shrubland (p=0.0024, p=0.0096, and p=0.0312, respectively).

3.2.2 Offspring fledging tarsus length

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Here, habitat type is also the sole variable significantly affecting the day 16 tarsus length (p<0.0001, figure 12).



Habitat type

The post-hoc analysis shows that the day 16 tarsus length of nestlings in the mid successional forest with understorey was significantly lower than that of nestlings in the mid successional forest without understorey and the mixed shrubland (p=0.0011, and p=0.0013, respectively). A trend was also found which indicated that nestlings in the mixed shrubland had a higher fledging tarsus length than nestlings in the early successional forest, but this was not significant.

3.2.3 Offspring fledging culmen length

It was found that both breast height tree diameter and the amount of deciduous tree positively significantly affect day 16 culmen length (p=0.013, and p=0.026, respectively; figure 13 and 14, respectively). Habitat type was found to not significantly affect day 16 culmen length.



Figure 13. Effect of the breast height tree diameter on the day 16 culmen length of the rayadito offspring.

Old growth forest

Mixed shrubland

Mid-suc. forest with understorey

Mid-suc, forest no understorey

The x-axis displays breast height diameter in centimetres and the v-axis shows the day 16 culmen length in millimetres.



Figure 14. Effect of the number of deciduous trees on the day 16 culmen length of the rayadito offspring.

The x-axis displays the number of deciduous trees and the y axis shows the day 16 culmen length in millimetres.

3.2.4 Offspring fledging body condition index

Lastly, here the model reveals that the fledging body condition index was significantly affected by habitat type (p=0.013, figure 15).



Conducting a post-hoc analysis on the different habitat types reveals that the underlying habitats do not differ significantly from one another.

4. Discussion

4.1 Habitat findings

To summarize findings here, it was generally found that habitat type affects rayadito offspring growth the most consistently. This goes for both the growth measures as well as the fledging measures, as all fitness measures except for fledging culmen length were found to be significantly affected by habitat type (figures 2, 5, 8, 9, 11, 12, and 15). This was not the only variable that affected the fitness measures, as for example body mass growth was also found to be affected by site and temperature (figures 3 and 4). Culmen length growth was also significantly affected by the former (7), whereas fledging culmen length was found to be affected by breast height tree diameter and the number of deciduous trees (figures 13 and 14). The tarsus length growth was found to be affected by diameter breast height (appendix 7.1) and the interaction between 0-3 metre and 5> metre foliage (figure 6). Lastly, the body condition index was also affected by 0-3 metre foliage, accumulated precipitation, and diameter breast height (figure 10, appendix 7.2, appendix 7.3 respectively).

Although almost all fitness measures were found to be significantly affected by habitat type, the direction in which this effect happened was less consistent across the different measures and thus potentially contradicting. For example, for the measures on the body condition index growth, the post-hoc analyses reveal that generally, nestlings in the mid successional forest with understorey had significantly higher growth and fledging measures than nestlings in other habitats (figures 5 and 9). However, for the culmen length growth, fledging body mass and fledging tarsus length, the post-hoc analysis shows that nestlings in the mid-successional forest with understorey have lower growth and fledging measure than those in other habitats (figures 8, 11, and 12

respectively). This should be taken with a grain of salt however, as this habitat is only ever significantly different from the mid successional forest without understorey and the mixed shrubland, rather than being different from all the other habitats. For instance, according to the models, the old growth forest does not differ significantly from any other habitats in any of the nestling growth and fledging measures. Nevertheless, these findings do put the focus on the mid successional forest as being either the best or the worst. However, from a biological perspective, this does not tell us much, as these are simply habitat categories and not actual environmental habitat factors that affect nestling growth.

4.2 Vegetation in context

Of course, as mentioned in the introduction, these habitat type differences are not the focus of this research, what we aimed to discover here are the underlying biotic and abiotic factor differences within these habitats. For instance, studies have found habitat differences, such as between the cityscape and agricultural land, but did not discover the underlying components causing these differences (Richner 1989). Although most findings here were based upon the habitat type differences, there were indications for underlying environmental factors causing these differences. Coming back to the habitat type differences, from the names alone, it can become evident that vegetation differences across these habitats can be quite substantial. The mid successional forest with understorey in particular potentially being the habitat with the densest vegetation. This could be explained by our findings on the other environmental factors, in particular those that are vegetation oriented. In fact, most of these are of positive nature. Literature suggests a positive relation between vegetation density and the abundance of secondary cavity-nesting birds (Tomasevic and Estades 2006), thus this relation could also be present for nestling growth. Here, the foliage coverage (both low and high), diameter breast height, and the number of deciduous trees all significantly positively affected several of the growth and fledging measures (figures 6, 10, 13, and 14). On the other side of the spectrum, however, diameter breast height was in two instances found to be negatively correlated with some growth and fledging measures (appendix 7.1 and 7.3). This is in contradiction to literature, which often points towards a positive relation between diameter breast height (as well as other vegetation measures) and food abundance (Basset 1999). It is important to note though, that these vegetation findings here on diameter breast height were often sparse and found only in specific fitness measures such as culmen length growth (appendix 7.1 and 7.3). However, they were also found for the residuals of the regression between body mass and tarsus length growth (body condition index growth), thus indicating that vegetation has this effect even on a combined structural size fitness measures such as these residuals.

Assuming this positive effect of vegetation, this can serve as an indication towards vegetation measures being a good predictor of habitat quality. In literature, several vegetation measures are often used as proxies for food abundance. In other studies focussed on insectivorous passerines, the prey items of these passerines are often determined by their preferred vegetation (Tremblay et al. 2005). For example, caterpillars prefer deciduous trees over evergreen trees, and thus knowing the distribution of these trees can serve as a predictor for caterpillar abundance and thus also for food abundance for several insectivorous passerines (Janzen 1993). On the other hand, certain spiders actually prefer evergreen trees over deciduous, and the density of these trees can affect their abundance as well (Gunnarsson 1990). In fact, most insects live from or on foliage, and thus more foliage often means more insects (Strong et al. 1984), which is also why the beatsheet method can predict general insect abundance throughout seasons so well (Wade et al. 2006). Thus, generally, vegetation measures can work well as habitat quality measures due to their predictive effect of

food abundance. In fact, this is why previous research took these measures into account and thus also why it was considered here, as a proxy for habitat quality.

Relating this to my hypotheses, the predictions on vegetation effects were found here, as I predicted these to be positively correlated. However, this effect works through food abundance, as I mentioned before, but unlike what I predicted, we found no evidence for an effect of food abundance here. A reason for this could be the choice of insect abundance measuring, the beat-sheet method. While this method by itself works great to predict seasonal differences in insect abundance, it works less well to predict specific insect abundances between habitats. This of course can be countered by constructing a nestbox specific measure such as the food index constructed here, which multiplied low foliage coverage (0-3 metres) by the insect abundance. However, this also did not significantly affect any of the fledging or growth measures. Nevertheless, while an effect of our measure of food abundance was not found, through these findings, vegetation can still serve as a good habitat quality measure through being a good predictor of food abundance. This can be quite crucial for future habitat choice-oriented research. Insect abundance is quite variable, changes throughout the season, and measuring this can be work intensive. Vegetation however is often static throughout nestling growth periods, and according to these findings and literature, can serve as a good predictor for habitat quality through its predictive effect of food abundance. Thus, for habitat choice-oriented research to focus on vegetation measures could not just potentially limit workload, but also offers alternative measures of food abundance for insectivorous passerines.

4.3 Future prospects

Despite most findings not focused on habitat type being vegetation oriented, it is not the only environmental factor we found here that affects the offsprings' growth. After all, we also found that body mass growth was affected by location and temperature (figures 3 and 4), as well as the former also affecting the culmen length growth (figure 7). Upon inspection of their respective graphs however, it becomes evident that the location and temperature effects are caused by the same points. Thus, the fact that temperature is affecting body mass is because of the effect of location, and potentially vice versa. While these findings demonstrate the effect of species being so widespread and can be important for future nestling growth focussed research, this effect is only found between the distant locations of Villarica and Navarino (figure 1), and not within unlike all previous vegetation findings. The vegetation findings are much more scattered throughout their graphs, making it evident that these are not caused by the location. Thus, for future studies focussing on growth (especially those in singular locations) it can be much more beneficial to focus on vegetation measures rather than temperature effects, as vegetation can differ tremendously on a small scale, whereas temperature often cannot.

On the subject of future studies, other aspects not included in this study are important to take into consideration as well. For instance, we were unable to take the sex of the nestlings into account. Given size has been found to differ among sexes due to intersex competition (among other reasons; Moreno et al. 2007), taking sex into consideration in the analyses would have corrected for this variation. However, unless we conducted genetic analyses on all nestlings, it was not possible for us to differentiate between the sexes. The same can be said for adult size, as previous studies have found a size difference between the two sites (Moreno et al. 2007), which in turn could also mean a difference in offspring fitness and reproductive success. Although we were unable to measure adults here, these findings from previous literature do indicate towards the importance of this measure for future research to take into account. While the findings do not unanimously point towards the effect of vegetation, it does indicate the importance of this environmental component for habitat quality determination. Our defined habitat types were the most often found factor affecting fitness measures. Although across different fitness measures the specific habitat differences were not the same, it did indicate towards habitats with the most vegetation having the highest growth and fledging measures. This argument was

further supported by other findings being mostly vegetation oriented. The importance of these findings is evidenced by its potential as a habitat quality measure through being a good food abundance predictor for insectivorous passerines. By taking vegetation effects and measures into account, future research could not only limit workload, but also amplify food abundance findings as certain vegetation measures can count as proxies for food abundance.

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7. Appendix

7.1: Chest height tree diameter effect on tarsus length growth

mentioned before in results section 3.1.2, tarsus length growth was found to be significantly affected by several factors including average chest-height tree diameter (p=0.024). This relation can be seen in figure 15.



Figure 15. Relation between tree diameter and tarsus length growth of the rayadito offspring.

The x-axis displays the breast-height tree diameter in centimetres and the y-axis displays the tarsus length growth



7.2: Precipitation effect on body mass & tarsus growth regression residuals

As mentioned in the results section 3.1.4, the residuals of the regression between body mass growth and tarsus length growth were significantly positively affected by accumulated precipitation (p=0.039). This relation can be seen in figure 17.



Figure 17. Relation between air temperature and tarsus length growth of the rayadito offspring.

The x-axis displays the air temperature in degrees Celsius and the y-axis displays the culmen

7.3: Tree diameter effect on body mass & tarsus growth regression residuals

As stated in results section 3.1.4, the residuals of the regression between body mass growth and tarsus length growth were significantly positively negatively by breast height tree diametre (p=0.018). This relation can be seen in figure 18.



Figure 18. Relation between air temperature and tarsus length growth of the rayadito offspring.

The x-axis displays the air temperature in degrees Celsius and the y-axis displays the culmen length growth.