

# Examining the potential trade-offs between postnatal parental allocation and various life history traits

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## **Abstract:**

This study uses the Mammalian Life History dataset to investigate trade-offs in the clade Euarchontoglires, focusing on the three orders Rodentia, Lagomorpha, and Primates. We focused on a post-birth parental allocation fraction (PAF) as a measure of resource allocation to reproduction, and compared PAF to various general life history traits to determine trade-offs. We ran linear mixed effects models to determine the statistically significant trade-offs for all three orders and the clade. The results illustrated significant ( $p < 0.05$ ) correlations exist in primates for PAF and weaning age, age at first reproduction, litters per year, litters per life, and total number of offspring. Two of the five observed significant correlations were negative correlations, and thus trade-offs. For the significant correlations we ran MANOVA to determine if Family was a significant predictor and also ran Multiple Comparison of Means with “Tukey” Contrasts to determine the differences between families with respect to both PAF and the given life history variable. The MANOVA test illustrated that Family was a significant predictor for all the correlations observed in primates and illustrated that Order was a significant predictor for the correlation observed in the clade. Significant clustering of families was demonstrated in all significant correlations except in the litters per life and litter size variables. This study demonstrates that, of the three orders studied, Primates are the only order in Euarchontoglires that experience trade-offs between parental allocation and general life history traits. The results of this study have implications for the theory of senescence.

## **Introduction:**

Evolution can be thought of as the optimization of systems based on environment and available variation in a population allowing for a change in trait frequency over time. However, these optimizations are often constrained by the optimization of other systems, resulting in what is referred to as a trade-off (Garland 2014). Trade-offs are common across all genera, from single-celled microorganisms (Novak et al. 2006) to large mammals (Gaillard et al. 2003). Optimization of a system includes the allocation of resources such as energy and nutrients - however, resources are limited for organisms, and so the resources used for one system may not then be available for another, presenting a trade-off in resource allocation (Stearns and Hoekstra 2005). The reproductive system is costly yet crucial system for an organism's fitness, allowing it to pass on genes to the next generation; however, getting to reproduction and being able to maintain the soma for caregiving and future reproduction are also costly. In mammals, there is a high level of parental allocation relative to other taxa, as all mammals produce milk to feed offspring, as well as give additional parental care such as protection from predation.

The superorder Euarchontoglires, which includes the orders Rodentia, Lagomorpha, and Primates, is a robust clade, with well-elucidated evolutionary relationships between these three orders (Asher and Helgen 2010). Primates and rodents in particular are well-studied, in part due to applications of research to human medicine and evolution. However, rodents and primates tend to have different life histories, with rodents generally having smaller body sizes, shorter lifespans, and larger and more frequent litters than primates. Lagomorphs, the rabbits and hares, are the sister group to rodents and share these characteristics. Lagomorphs and rodents, both phylogenetically and in life history, are more similar to each other than to primates, and so may have evolved more similar trade-offs based on these relationships. Thus, we will be

utilizing the orders Rodentia, Lagomorpha, and Primates, which are evolutionarily similar and with clear inter-order relationships, to test various life history trade-offs with respect to reproduction. While the orders Scandentia and Dermoptera are included in Euarchontoglires as a sister group to Primates, we have omitted them in our analysis due to their relative rarity. We will be focusing on post-birth parental allocation as a measure of resource allocation to reproduction, and comparing this to various somatic and reproductive life history characteristics.

The specific aim of this research is to take an exploratory approach and investigate if trade-offs are observed between investment in various general life history traits compared to parental allocation of resources to offspring in a mammalian system. We designed the parental allocation fraction (PAF) variable as a measure for investment in reproduction, and compared this variable to general life history traits. We investigated relationships in the super clade, between orders, and within families of orders we found significant correlations in. Every trade-off investigated compared a general somatic or reproductive life history characteristic to parental allocation. We investigated if trade-offs existed between PAF and the following general life history traits; Maximum Life Span, Life Span Scaled Age at First Reproduction, Number of Litters per Year, Average Litter Size, Life Span Scaled Average Gestation Length, Number of Litters per Life, Average Total Offspring, Life Span Scaled Average Weaning Age, and Total Number of Offspring per Life. As we took an exploratory approach to this research, therefore we tested the null hypothesis that no correlation existed between investment in parental allocation for reproduction and other life general history traits. We investigated all the significant correlations we observed from the linear models, but only classified the negative correlations as trade-offs.

## **Methods:**

### ***Data description:***

We utilized the public dataset of Mammalian Life History compiled by S. K. Morgan Ernest, published in 2003 in the journal Ecology. The dataset is intended for life history comparisons, and contains relatively complete information for Euarchontoglires. Variables included in the dataset are: maximum life span (months), age of first reproduction (months), gestation time (months), weaning age (months), weaning mass (grams), litter size, litters per year, new born mass (grams), and adult body mass (grams). All variables are relevant for our analysis, and used as proxies for resource allocation towards reproduction and to the soma.

The data set was updated to place species into the correct families based on the most recent molecular phylogeny of the order primates (Perelman et al. 2011).

### ***Data manipulation:***

Parental allocation was quantified utilizing body mass gained by an offspring during the parental care period (prior to weaning) scaled by adult body mass so as to account for overall growth. This resulted in the Parental Allocation Fraction (PAF), calculated as follows utilizing the information available in the dataset:

$$\text{parental allocation fraction (PAF)} = \frac{\text{weaning mass} - \text{newborn mass}}{\text{adult body mass}}$$

Additional scaling was also applied to weaning age, average age at first reproduction, and gestation period (both scaled by maximum lifespan so as to control for differences in overall lifespan) as follows:

$$\begin{aligned}
 \text{scaled weaning age} &= \frac{\text{weaning age}}{\text{maximum lifespan}} \\
 \text{Scaled average age at first reproduction} &= \frac{\text{average age of first reproduction}}{\text{maximum lifespan}} \\
 \text{scaled gestation time} &= \frac{\text{gestation time}}{\text{maximum lifespan}}
 \end{aligned}$$

Litters per life was calculated as a measure of overall reproductive output across the lifespan, and was calculated as follows:

$$\text{litters per life} = \text{litters per year} \left( \frac{\text{maximum lifespan (mo)} - \text{average age at first reproduction (mo)}}{12} \right)$$

Average Total Offspring per Life was calculated as follows:

$$\text{total offspring} = \text{litters per life} \times \text{litter size}$$

Due to the nature of scaling and calculation, only species with adequate data available were included in our analyses.

### ***Description of Statistical Analyses:***

All statistical analyses were conducted in R studio, version 1.1.456. We ran linear models to determine the relationship between the PAF and the eight life history traits, three of which were scaled with respect to maximum life span within species (Average Age at Reproduction, Average Gestation Length, and Average Weaning Month). For each relationship we ran several linear models; one that looked at all species within the clade Euarchontoglires in which Family was instituted as a random effect within the model, three linear models for the Orders Lagomorpha, Primates, and Rodentia, and a linear model for the clade Euarchontoglires in which Family was included as a nested effect within Order. We chose to exclude Dermoptera and Scandentia due to insufficient number of species, preventing our ability to make relevant conclusions.

Based on relevant knowledge gained from the previous linear models we then built clustered hull plots for the significant correlations observed in the order Primates as well as for the superorder Euarchontoglires. In these cluster hull plots the points were put into hulls based on the Family in which the species pertain to. We then ran MANOVA to determine if Family was a significant predictor of the relationship between PAF and the given life history variable. We also ran a Multiple Comparison of Means with “Tukey” Contrasts to determine the differences between families with respect to both parental allocation and the given life history variable.

### **Results:**

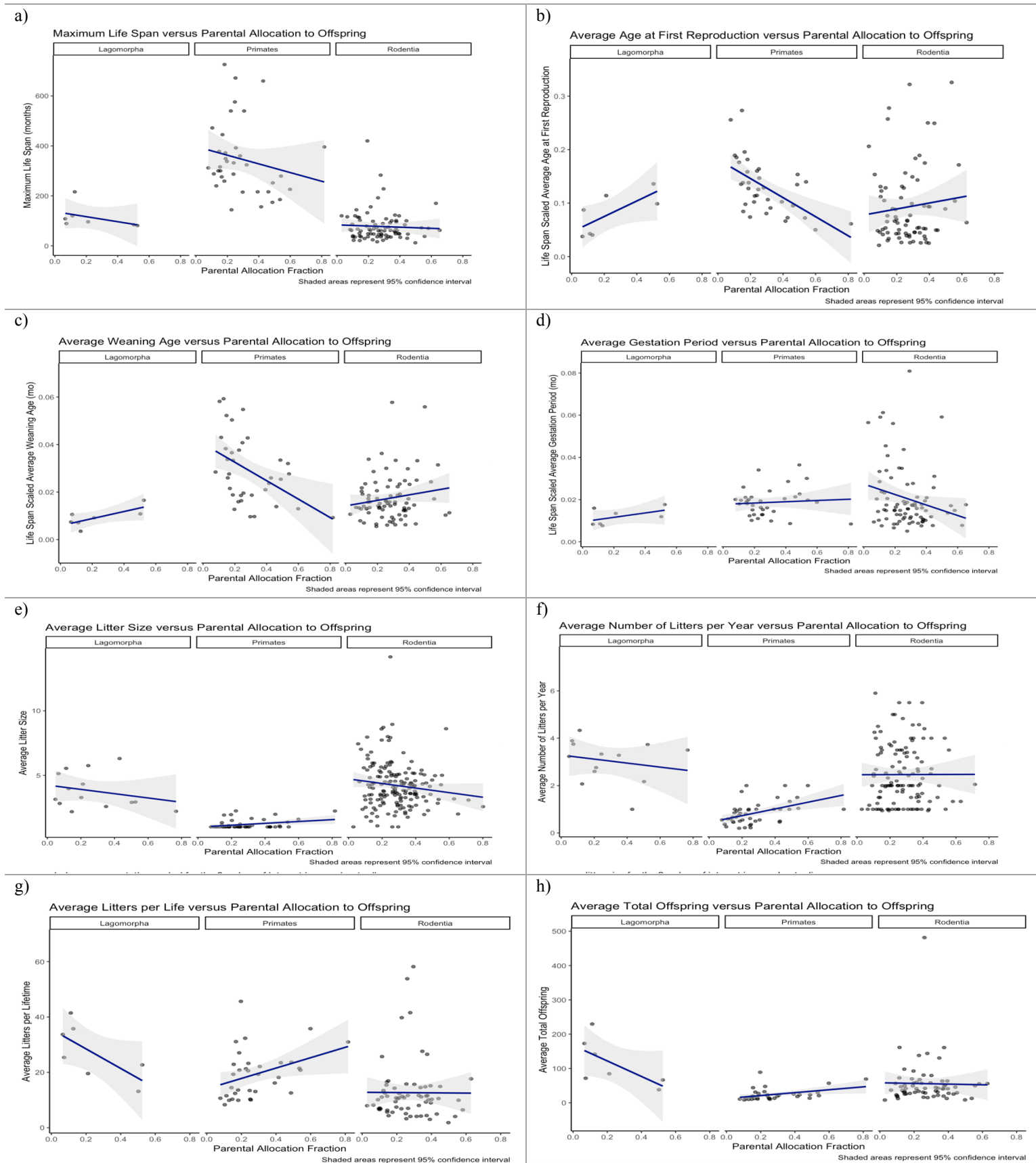


Figure 1a-h: Linear regression graphs investigating the correlation between parental allocation and various general life history traits, in the orders Lagomorpha, Rodentia, and Primates from the clade Euarchontoglires. a) correlation between parental allocation fraction and maximum life span, not significant in any order. b) correlation between parental allocation and life span scaled average age at first reproduction, only significant ( $p < 0.01$ ) in primates. c) correlation between parental allocation and life span scaled average weaning age, only significant ( $p < 0.01$ ) in primates. d) correlation between parental allocation and life

span scaled average gestation period, not significant in any order. e) correlation between parental allocation and average litter size, not significant in any order. f) correlation between parental allocation and average number of litters per year, only significant ( $p < 0.01$ ) in primates. g) correlation between parental allocation and average litters per life, only significant in primates ( $p < 0.05$ ). h) correlation between parental allocation and total offspring per life, only significant in primates ( $p < 0.05$ ).

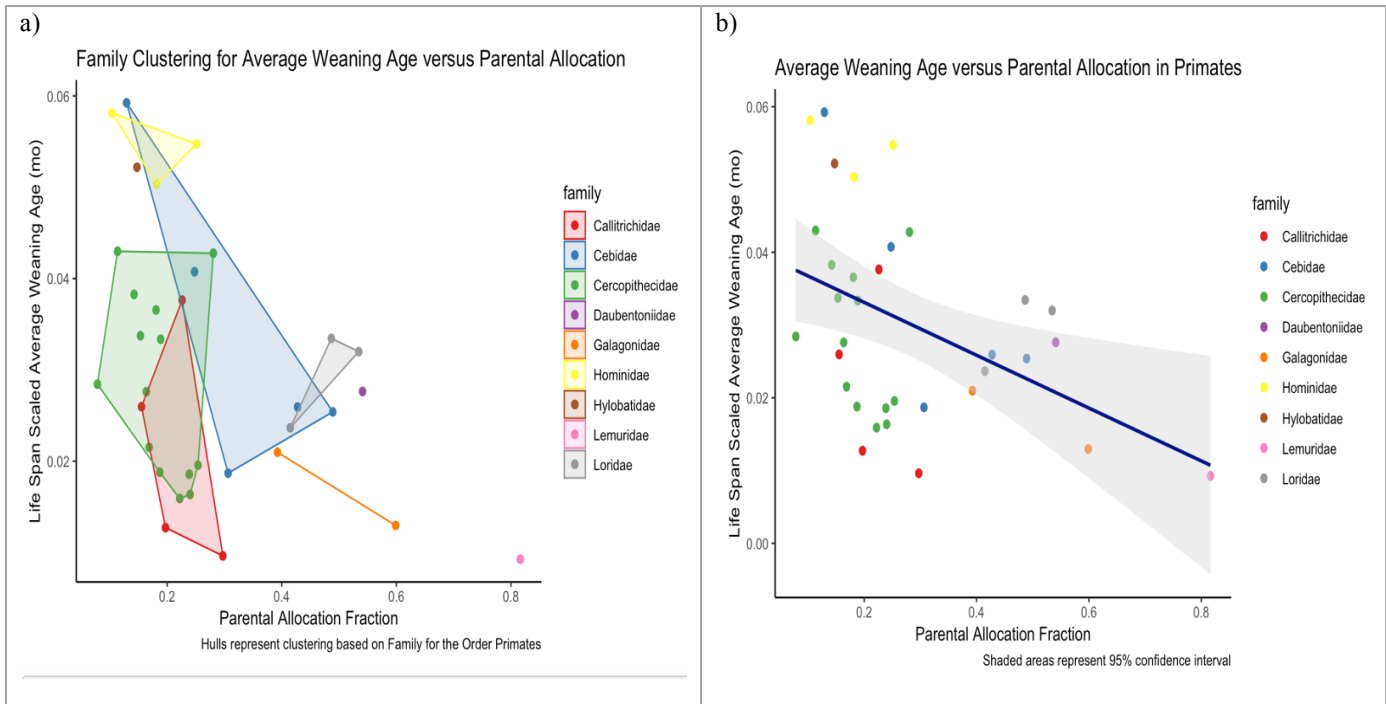


Figure 2a-b: a) Cluster hull plot for significant ( $p < 0.01$ ) relationship observed in primates between life span scaled average weaning age and parental allocation. Hull plot is clustered by families within the primate order. b) Linear regression showing the significant ( $p < 0.01$ ) relationship between life span scaled average weaning age and parental allocation in primates by families.

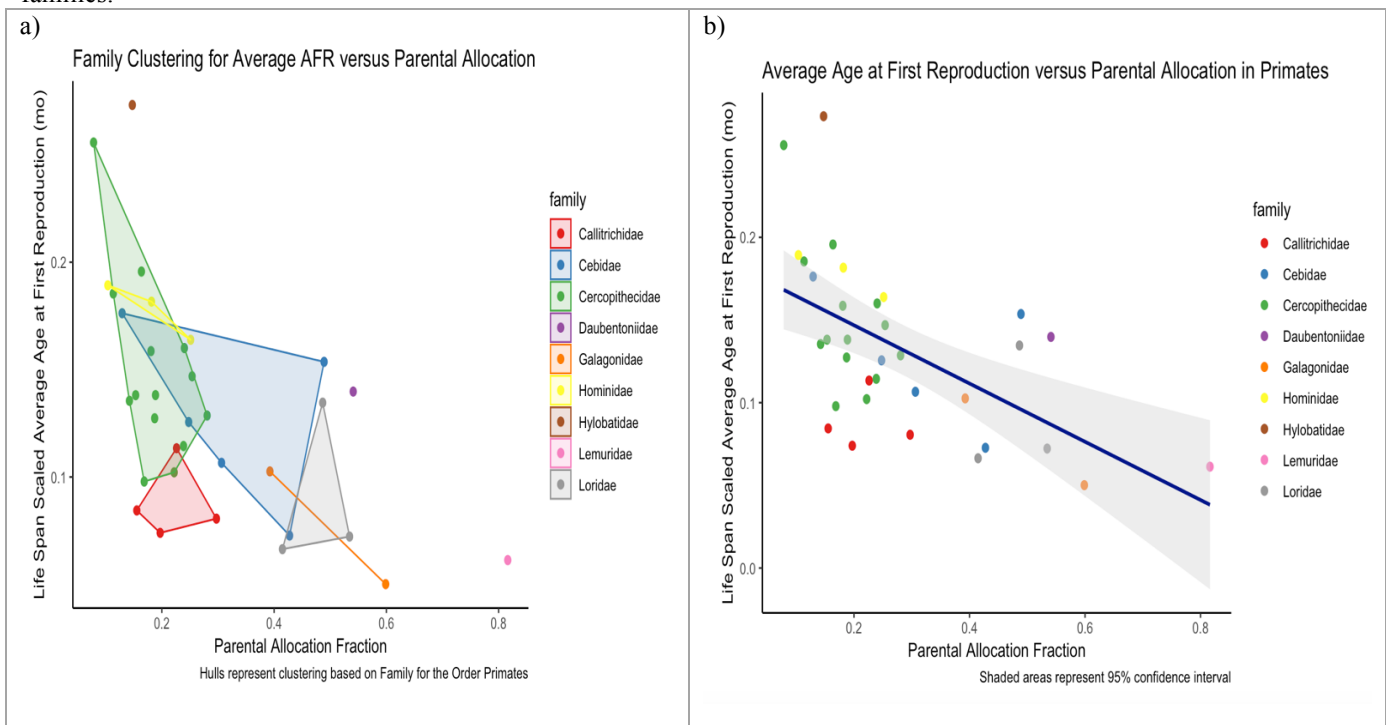


Figure 3a-b: a) Cluster hull plot for significant ( $p < 0.01$ ) relationship observed in primates between life span scaled average age at first reproduction and parental allocation. Hull plot is clustered by families within the primate order. b) Linear regression showing the significant ( $p < 0.01$ ) relationship between life span scaled average age at first reproduction and parental allocation in primates by families.

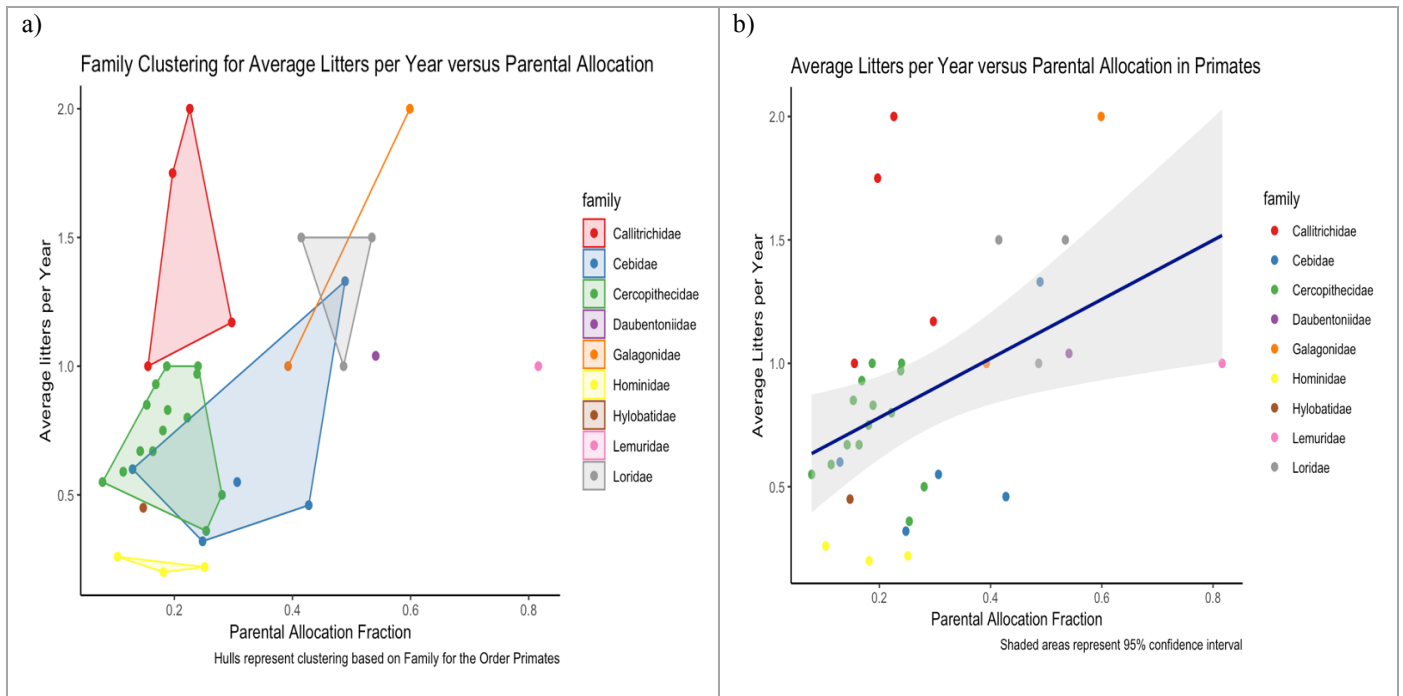


Figure 4a-b: a) Cluster hull plot for significant ( $p < 0.01$ ) relationship observed in primates between average number of litters per year and parental allocation. Hull plot is clustered by families within the primate order. b) Linear regression showing the significant ( $p < 0.01$ ) relationship between average number of litters per year and parental allocation in primates by families.

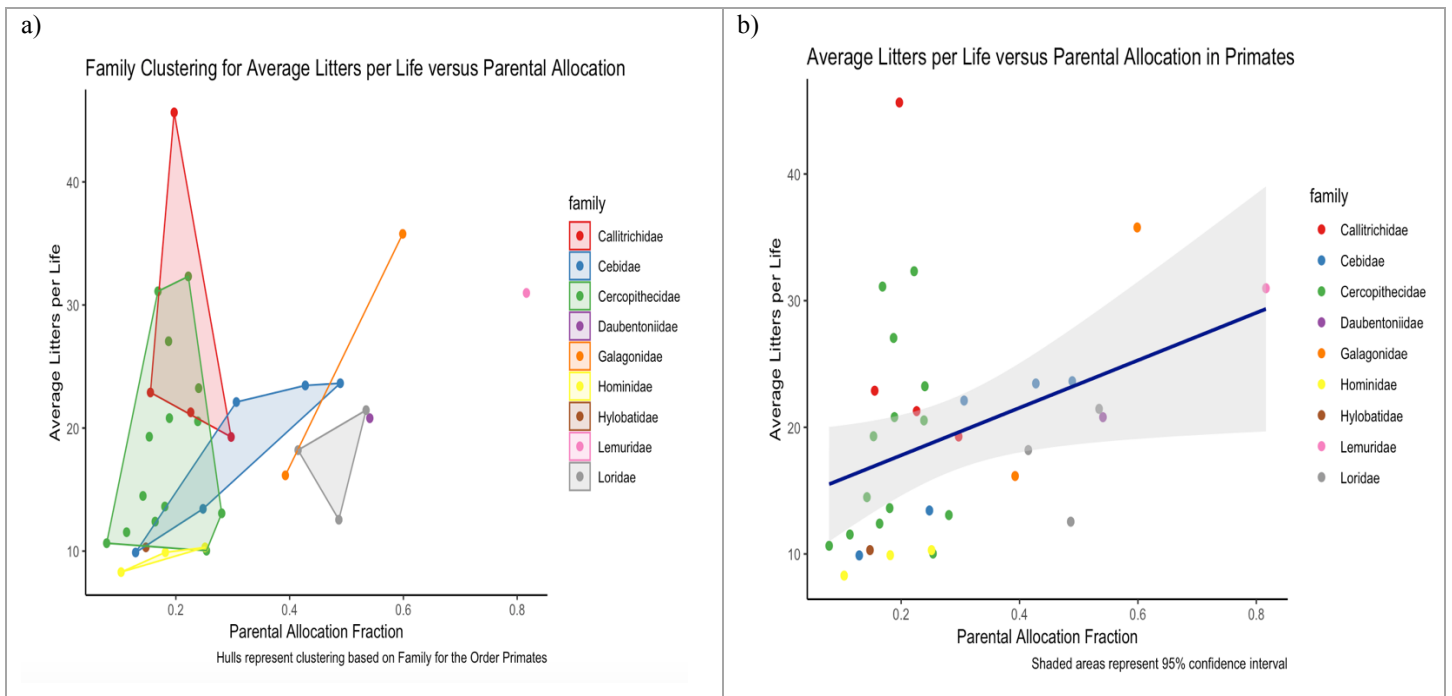


Figure 5a-b: a) Cluster hull plot for significant ( $p < 0.05$ ) trade-off observed in primates between average number of litters per life and parental allocation. Hull plot is clustered by families within the primate order. b) Linear regression showing the significant ( $p < 0.05$ ) trade-off between average number of litters per life and parental allocation in primates by families.

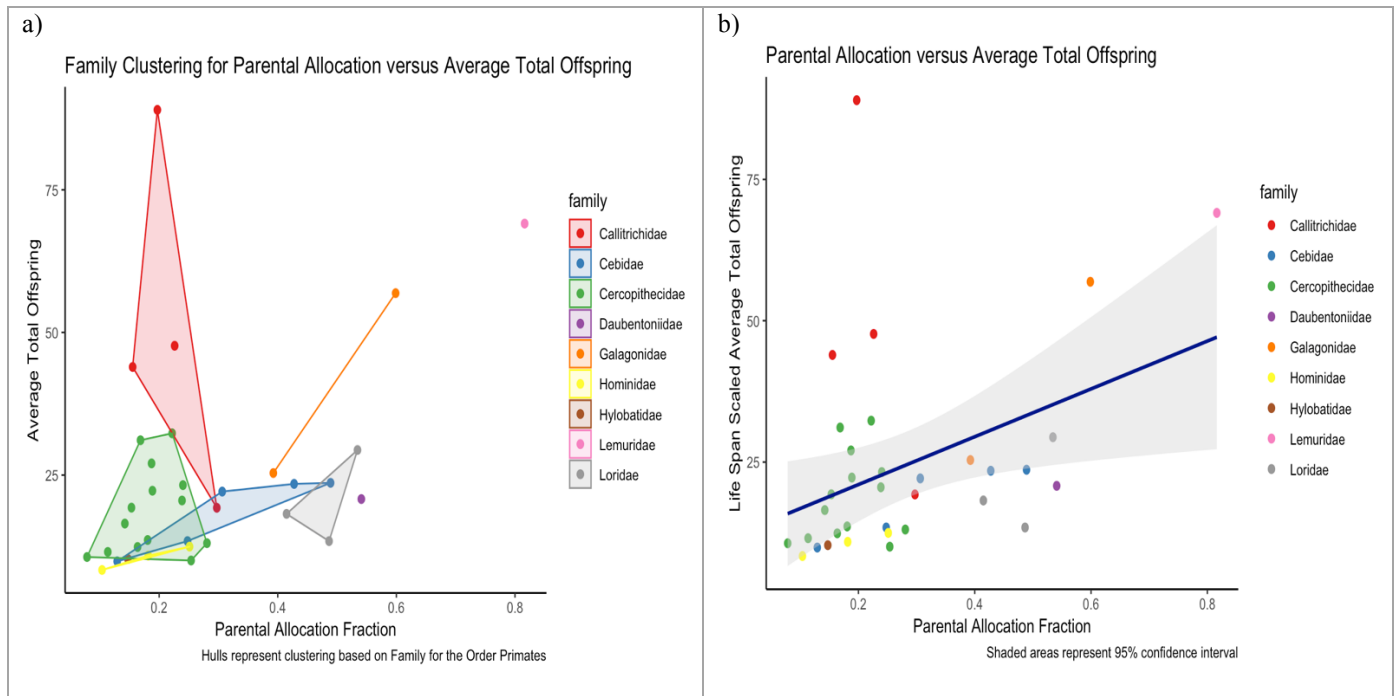


Figure 6a-b: a) Cluster hull plot for significant ( $p < 0.05$ ) trade-off observed between total number of offspring per life and parental allocation in primates. Hull plot is clustered by families. b) Linear regression showing the significant ( $p < 0.05$ ) tradeoff between e total number of offspring per life and parental allocation in primates by family.

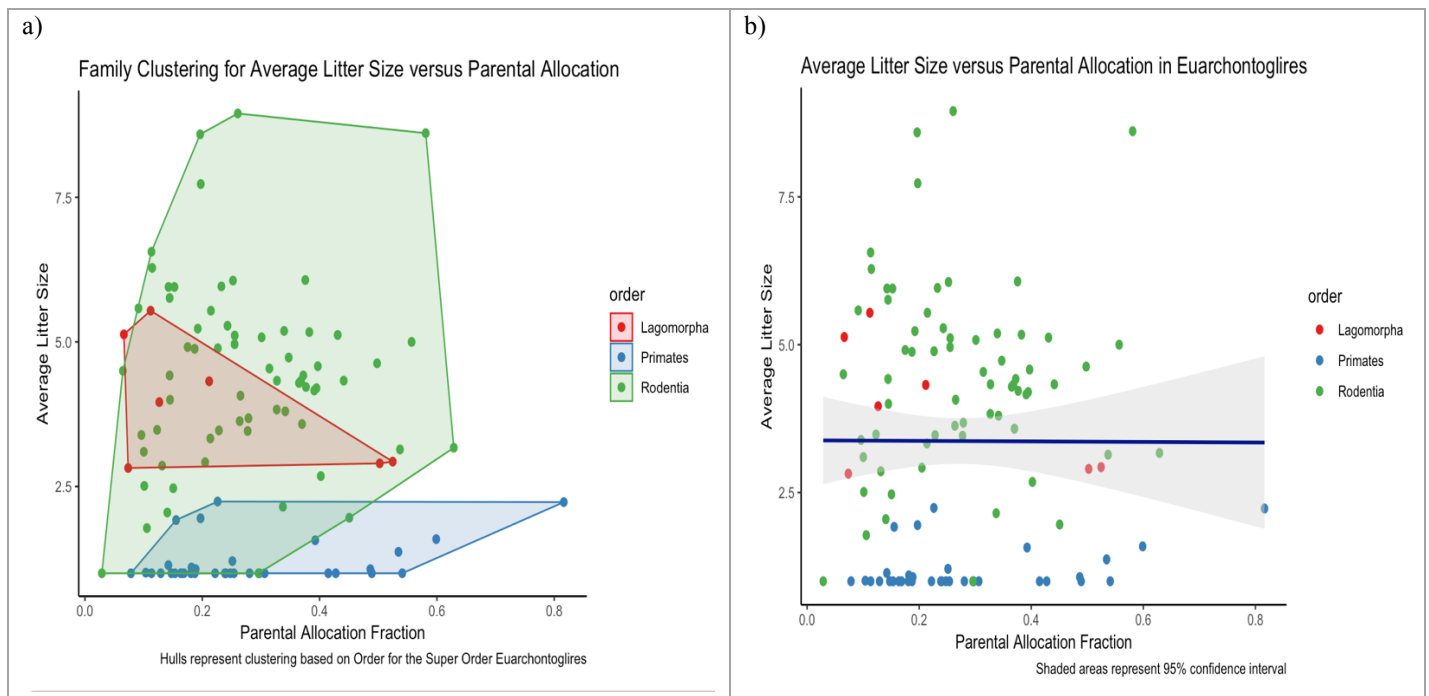


Figure 7a-b: a) Cluster hull plot for significant ( $p < 0.05$ ) relationship observed in the super order Euarchontoglires between average litter size and parental allocation. Hull plot is clustered by orders. b) Linear regression showing the significant ( $p < 0.05$ ) relationship between average litter size and parental allocation in the super order Euarchontoglires by order.



### ***Linear Regressions and Superorder Scatter Plots:***

In the linear regressions of the scatter plots of Euarchontoglires and its three largest orders, Lagomorpha, Primates, and Rodentia, we found several significant relationships. When looking at how the PAF predicts species Maximum Life Span (Figure 1a) we found no significant correlations to exist. However, the linear models showing how PAF predicts the Life Span Scaled Average Age at First Reproduction (Figure 1b) we found that in the model for Primates where the family was a random effect there was a significant negative correlation ( $p < 0.01$ ). This was also similar in the nested effect of family model where the order Primates showed a significant negative correlation between PAF and Life Span Scaled Average Age at First Reproduction ( $p < 0.05$ ). When looking at how PAF predicts Life Span Scaled Average Weaning Age we found no significant correlations via any of the linear models (Figure 1c). In the linear models for how PAF predicts Life-Span Scaled Gestation Length (Figure 1d) we found no significant correlations in any of the models. Similarly, for the linear model for how PAF predicts Average Litter Size (Figure 1e) we found no significant correlations in any of the Order specific models. However, there was a significant correlation across the superorder Euarchontoglires when Family was included as a random effect ( $p < 0.05$ ) but this correlation was not significant in the model where family was included as a nested effect within Order. In the linear model for how PAF predicts the Average Number of Litters per Year (Figure 1f) there was a significant positive correlation in the linear model with family as a random effect for Primates ( $p < 0.01$ ) and in the family as a nested effect model for Euarchontoglires ( $p < 0.01$ ). In the linear models where we looked at how PAF predicted Average Litters per Lifetime (Figure 1g) there was again a significant positive correlation in the Primates model with family as a random effect ( $p < 0.05$ ) and in the nested effect of family model for the superorder there was also a significant positive correlation in Primates ( $p < 0.05$ ). The linear model for how PAF predicted Total Offspring per Life (Figure 1h) showed significant positive correlation in Primates ( $p < 0.05$ ). As well, the linear model in which Family was nested within Order across the whole superorder also showed a significant positive correlation for Primates ( $p < 0.05$ ).

### ***Cluster Hull Plots and post-hoc Analysis:***

Based on the results of the linear analysis we then took the significant correlations, which all occurred in the Order Primates, and created hull graphs and ran post-hoc tests to see if there was visible clustering within Families and if the clusters were significantly different. When looking at how PAF predicts Life Span Scaled Average Weaning Age in Primates (Figure 2a-b) we found via MANOVA that Family was a significant ( $p < 0.001$ ) predictor of both variables. Following this we ran a Multiple Comparisons of Means: “Tukey” Contrasts for how Family predicts both PAF and Life Span Scaled Average Weaning Age (2-Dimensional) and found that there were significant cluster differences between the Families Hominidae and Galagonidae ( $p < 0.05$ ) and Hominidae and Lemuridae ( $p < 0.05$ ). When looking at how PAF predicts Average Age at First Reproduction in Primates (Figure 3a-b) we found via MANOVA that Family significantly predicted the relationship ( $p < 0.001$ ). When running a Multiple Comparisons of Means: “Tukey” Contrasts (2-Dimensional) we found significant cluster differences between the Families Hylobatidae and Galagonidae ( $p < 0.05$ ), Hylobatidae and Lemuridae ( $p < 0.05$ ) and Hylobatidae and Loridae ( $p < 0.05$ ). Moreover, looking at how PAF predicts Average Number of Litters per Year in Primates (Figure 4a-b) we found via MANOVA that Family was a significant predictor of the relationship ( $p < 0.001$ ). Through the “Tukey” Comparison Testing (2-Dimensional) we witnessed significant clustering differences between the Families Hominidae and Galagonidae ( $p < 0.01$ ) as well as Hominidae and Loridae ( $p < 0.01$ ). Similarly, when looking at how PAF predicts Average Number of Litters per Lifetime in Primates (Figure 5a-b) MANOVA testing showed us that Family significantly predicted the relationship ( $p < 0.001$ ). However, the Multiple Comparison of Means: “Tukey” Contrasts



(2-Dimensional) Testing showed no significant clustering differences between any of the Families. Furthermore, when examining how PAF predicts Average Total Offspring in Primates (Figure 6a-b) MANOVA showed that Family significantly predicted the relationship ( $p < 0.001$ ). By running the Multiple Comparisons of Means: “Tukey” Contrasts we found significant clustering differences between the families Lemuridae and Cebidae ( $p < 0.05$ ), Lemuridae and Cercopithecidae ( $p < 0.05$ ), and Lemuridae and Hominidae ( $p < 0.05$ ). When running a MANOVA on how PAF predicts Average Litter Size throughout the superorder Euarchontoglires (Figure 7a-b) we found that Order was a significant predictor. However we then ran Multiple Comparisons of Means: “Tukey” Contrasts (2-Dimensional) on the relationship there were no significant clustering differences between the various Orders.

## **Discussion:**

Our study revealed significant relationships between the parental allocation fraction and scaled weaning age (Figures 1c, 2b), average age at first reproduction (Figures 1b, 3b), total offspring (Figures 1h, 6b), and litters per life (Figures 1g, 5b) and year (Figures 1f, 4b) in Primates. A significant relationship was observed for all three orders together between PAF and average litter size, however the relationship was neutral and there was no significant difference between orders (Figure 7a, b). Trade-offs (negative correlations) were observed for PAF and Life Span Scaled Average Weaning Age and PAF (Figure 2b) and Life Span Scaled Age at First Reproduction (Figure 3b). From this, we can see that increased parental allocation allows for quicker maturation of offspring in Primates, and thus increased overall reproductive output in number of litters per year, litters per life, and total offspring produced. Families with greater parental allocation tend to wean and reproduce earlier in the lifespan (Figure 2a-b, 3a-b). Earlier weaning indicates that the offspring of Primates with greater parental allocation mature to a size such that they can survive without continued parental resources quicker than species with lower parental allocation. Our results also show that in Primates, parental allocation is negatively correlated with Average Age of First Reproduction (Figure 3 a-b). Thus, the more parental allocation a Primate family provides, the younger that family would reproduce. This result is consistent with findings reported by Hawkes et al (2003) that indicated that when mothers provide more food to their offspring, those daughters have higher fecundity. Primates also showed a positive relationship between PAF and the number of litters produced per year and over the lifetime, as well as total offspring produced. Early maturation would contribute to the increased lifespan reproductive output, as the reproductive period is increased.

Our study showed differences between Primate families consistent with known Primate life history tendencies. Larger-bodied species tend to live “slower” (Hawkes et al., 2003): this includes higher age of maturity (weaning age and age at first reproduction) and lower fecundity (litter frequency and total offspring), especially in Hominidae. This lower maturity can be observed in Figure 2a in which there was a significant difference in PAF and weaning age among families, such as the family Hominidae having a distinctly older weaning age compared to other families such as Galagonidae, which are significantly smaller than Hominids. Lower fecundity can be seen in figures 4a, 5a, and 6a, as the Hominidae family shows the least number of litters per year, litters per lifetime, and total offspring. The Hominidae family shows the lowest fecundity in litters per year, litters per lifetime, and total offspring produced, which could be attributable to higher somatic investment (Hill and Kaplan 1999), as seen by the tendency of Hominids to live longer and have larger bodies than other Primate families. Larger investment of energy into body mass allows for senescence to occur at a later age (Hill and Kaplan 1999) in accordance with the disposable soma theory of senescence (Kirkwood and Holliday 1979). The disposable soma theory indicates that ageing occurs as a result of resource allocation away from somatic maintenance towards other aspects such as reproduction (Kirkwood and Holliday 1979, Heuvel et al. 2016). This may be seen if increased reproductive output or parental allocation resulted in decreased

lifespan or other somatic traits (Heuvel et al. 2016), however we did not find any effects of parental allocation on lifespan, contrary to the disposable soma theory.

The null effect seen between PAF and lifespan may be explained by the Grandmothering hypothesis, which says that a grandparent without nurslings can provision to grandchildren after weaning, thus releasing the mother from the need to allocate as much resource to their offspring and therefore allow the mother to produce the next offspring quicker (Hawkes et al. 2003). This can result in selection for increased, possibly postmenopausal, lifespan. The Grandmothering effect could act to balance the senescence effects of the disposable soma theory, resulting in the null relationship seen between parental allocation and lifespan. Additionally, Grandmothering prior to weaning or any investment from non-parent kin (in forms other than milk, such as oversight/protection, or gathering food for the mother) could explain why PAF is higher in families with greater fecundity (litters per year, litters per lifetime, and total offspring). Offspring are receiving resources from different relatives of multiple generations, therefore increasing perceived parental allocation (calculated as PAF; see *Methods*). However, in fact, the parent is providing reduced provisions to allow for quicker production of the next litter. Offspring weaning age determines the rate of offspring production, as weaning releases the mother from current parental allocation so that she can allocate resources to future offspring (Hawkes et al., 2003). This can be seen in Figure 3b, 4b and 5b as the higher the parental allocation fraction, the higher the family's fecundity as indicated by earlier age of reproduction and greater litters per year, lifetime, and total offspring. As discussed, fecundity and earlier maturity tend to be seen in small-bodied Primate families, so future research could look to examine Grandmothering and other non-parental investment across Primates of different somatic investments (body sizes). However, the null effect between lifespan and PAF could be more related to predation risk that somatic investment: smaller-bodied Primates tend to experience greater predation, and individuals with a higher probability of predation will invest less energy into cellular repair, instead allocating that energy to offspring (Hill and Kaplan 1999). Further research should therefore look into body size correlations in Primates to investigate somatic-reproductive tradeoffs with respect to both the disposable soma theory and predation risk.

### ***Limitations:***

Due to the nature and scaling of our data after wrangling, only species with adequate data were included in our analysis. The orders Scandentia and Dermoptera had inadequate amounts of data, therefore these two orders from Euarchontoglires were excluded from our analysis. Although we can extrapolate the role of humans with respect to the various life history trade-offs as part of Hominidae, we caution against making direct conclusions as *Homo sapiens* were not an included species within our dataset. Included in the Hominidae dataset were our most closely related genus, Pan (chimpanzees and bonobos), which allows for extrapolation of results to humans. Further research is needed to generalize our results to *Homo sapiens*. Finally, the results of this study should not be generalized to individuals, as the dataset was comprised of averages for life history traits, making the results only truly relevant to the order, family, or species level.

### **Conclusion:**

Utilizing data from the Mammalian Life History dataset, we investigated possible life history trade-offs between postnatal parental allocation to reproduction and other somatic and reproductive traits for the three largest orders within the clade Euarchontoglires, and found five different significant correlations between parental allocation and various life history traits, abide only in Primates. This research found two trade-offs, between PAF and the age at first reproduction and PAF and weaning age.

We found Family to be a significant predictor for these relationships between PAF and various life history traits. Our cluster graphs and post-Hoc tests illustrated significant differences between families, which was consistent with known primate life history tendencies. The results of this research have implications for senescence theory, specifically pertaining to the Grandmothering hypothesis and disposable soma theory, and confirm the life history tendencies within Primates. Further studies could seek to elucidate what fraction of resources are allocated by different generations, as well as determine if other measures of reproductive investment have effects on somatic traits such as lifespan.

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