Analysis of Life History Traits and Their Relationship with Reproductive Output in Aves, Mammalia and Reptilia

EEB313
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Abstract

Reproductive output is a widely studied topic in the field of ecology and has been shown to be a determining factor in species sensitivity to habitat loss. Due to this, insight into variables related to reproductive output can help further our understanding of what makes certain species more vulnerable than others. Analysis of 8 different parameters related to species development was undertaken in order to determine if any were correlated with reproductive output. Results showed a negative correlation among all traits which was consistent with current literature and expected under life history theory.

Introduction

Explaining variation in reproductive output is an interesting problem in the field of ecology and many papers have been written contributing to our collective knowledge on the topic. Despite some variation being explained by factors such as latitude (Evans et al. 2009), nutrition (Cooke, F. et al. 1990) and seasonality (Evans et al. 2009), much of this variation is still unexplained. Furthermore, studies on this topic often focus on the species level and seldom look at different factors in conjunction with one another. Low reproductive rate has been shown to be correlated with sensitivity to habitat loss (Quesnelle et al. 2014). Therefore, by identifying which traits are correlated to reproductive rate we can better identify which species may be more sensitive to habitat loss and therefore more at risk of extinction. Specifically, the relationship between reproductive output among Aves (birds), Mammalia (mammals) and Reptilia (reptiles) and adult body mass, longevity, female/male maturity time, incubation time, fledging age, adult svl, and weaning time will be examined to help better identify which groups of species will be at higher risk of extinction.

Life history theory suggests a fundamental tradeoff between number of offspring and developmental traits such as size, longevity and maturity time. (Walker et al. 2007). Current literature supports this theory with one example being the relationship between size, maturity time and fecundity within North American fish species (Winemiller and Rose, 1992). Life history theory would suggest a negative correlation between all developmental traits examined and reproductive output across all classes and therefore this is the predicted result of our analysis. Based on this, it was hypothesised that reproductive output (offspring produced per year) would be correlated with at least one of developmental traits. Furthermore, the null hypothesis is that reproductive output has no correlation with developmental traits. Overall, the objective of this analysis was to determine if there is correlation between reproductive rate and any of the developmental traits analyzed.

Methods

1. Data Sources

The dataset used for analysis was 'An amniote life-history database to perform comparative analyses with birds, mammals, and reptiles' composed by N.P. Myhrvold, E. Baldridage, B. Chan, D.Sivam, D.L. Freeman and S.K. Morgan-Ernest. It was published in volume 96, issue 11 of the journal *Ecology* in November 2015.

The authors first developed this dataset to deal with the problem of life-history data of amniote species being split among various publicly available databases and data tables embedded in individual papers and books. Species-specific studies by experts, which made large-scale macroecological studies challenging because of a lack of standardization in taxonomic classifications, parameter values, and even in which parameters are reported (Myhrvold et al. 2015). The motivation for developing this dataset was to "facilitate comparative analyses between amniote life-history data," as described by the authors.

The authors first extracted raw data from peer-reviewed studies, existing databases, published books and other compilations. Then they corrected all spelling errors and adjusted data to accommodate species transformation(species promotion, demotion, merge etc.). Finally, the median value was recorded for species with parameters containing more than one data point. The product is a large-scale database containing 29 life-history parameters for 21322 species of birds, mammals and reptiles.

The purpose of our analysis is to examine the relationship between reproductive output and a variety of development traits. This makes this dataset ideal as not only is there data for over 20000 species across 3 different classes, but there are also 29 parameters which can be examined (27 when excluding reproductive output parameters).

2. Data manipulations

All the data manipulations were conducted using RStudio with R version 4.2.1 (R core team, 2022).

First, we extracted the parameter "litter_or_clutch_size_n" and "litters_or_clutches_per_y" from the database and multiplied these two, which gave us the parameter representing the annual offspring produced.

Second, we separated the raw database into three sub-datasets, each containing a class of amniotes (birds, mammals, reptiles).

Third, we selected most parameters in the dataset that are related to the research topic, and we removed all the parameters that contained unknown or invalid data points.

Fourth, we removed an outlier from the Aves sub-dataset. The removed species is the Australian Brush Turkey which had an annual offspring produced of over 300. This value does not make biological sense and therefore it is believed this abnormality was caused by a data entry error when the database was created.

3. Statistical Analyses

All the data analyses were conducted using RStudio with R version 4.2.1 (R core team, 2022).

We first conducted a series of correlation tests on each taxa group to test the collinearity assumption using the function "corr. test" from R package "psych" (Revelle, 2022). Among all the highly correlated parameters, we selected one parameter as representative of the group, and used the selected parameter in the PCA to avoid collinearity..

After the correlation test, we decided to perform a series of Principle Component Analyses (PCA) tests on each class to find any relationship between our response variable, the annual reproductive output, and our multiple predictors.

Results

1. Aves

The result from the correlation test revealed that many parameters are heavily correlated with each other (Fig1). Adult body mass is highly correlated to adult svl, egg mass and birth weight, among all these parameters, adult body mass was selected as the representative parameter.

```
Call:corr.test(x = aves_avg_bodysize[, 6:16], method = "pearson")
Correlation matrix
                        adult_body_mass_g longevity_y litter_or_clutch_size_n adult_svl_cm egg_mass_g litters_or_clutches_per_y
adult_body_mass_g                    1.00        0.58                   -0.15         0.87       0.94                     -0.17
longevity_y                          0.58        1.00                   -0.20         0.60       0.55                     -0.07
litter_or_clutch_size_n             -0.15       -0.20                    1.00        -0.07      -0.13                     -0.04
adult_svl_cm                         0.87        0.60                   -0.07         1.00       0.87                     -0.20
egg_mass_g                           0.94        0.55                   -0.13         0.87       1.00                     -0.20
litters_or_clutches_per_y           -0.17       -0.07                   -0.04        -0.20      -0.20                      1.00
female_maturity_d                    0.67        0.52                   -0.45         0.63       0.68                     -0.17
male_maturity_d                      0.64        0.52                   -0.42         0.62       0.64                     -0.15
birth_or_hatching_weight_g           0.95        0.58                   -0.19         0.86       0.98                     -0.20
incubation_d                         0.53        0.34                   -0.16         0.54       0.61                     -0.21
fledging_age_d                       0.77        0.62                   -0.11         0.70       0.81                     -0.25
                        female_maturity_d male_maturity_d birth_or_hatching_weight_g incubation_d fledging_age_d
adult_body_mass_g                    0.67            0.64                       0.95         0.53           0.77
longevity_y                          0.52            0.52                       0.58         0.34           0.62
litter_or_clutch_size_n             -0.45           -0.42                      -0.19        -0.16          -0.11
adult_svl_cm                         0.63            0.62                       0.86         0.54           0.70
egg_mass_g                           0.68            0.64                       0.98         0.61           0.81
litters_or_clutches_per_y           -0.17           -0.15                      -0.20        -0.21          -0.25
female_maturity_d                    1.00            0.97                       0.71         0.45           0.70
male_maturity_d                      0.97            1.00                       0.67         0.37           0.68
birth_or_hatching_weight_g           0.71            0.67                       1.00         0.61           0.81
incubation_d                         0.45            0.37                       0.61         1.00           0.48
fledging_age_d                       0.70            0.68                       0.81         0.48           1.00
Sample Size
```

Figure 1. This image shows the result of the Aves correlation test. It shows that many parameters are heavily correlated to each other. The absolute value indicates the level of correlation, and the + or - sign represents the direction of the correlation.

In the Principle Component Analysis (PCA) of the Aves (Fig 2a), PC axis 1 and PC axis 2 captured 79.2% of all the variations of the Aves life-history traits. Adult body mass, average longevity, fledgling age and time to reach maturity are positively correlated to the PC1 axis; incubation alone is positively correlated to the PC2 axis. Most Aves species are concentrated near the zero-value region of both the PC1 and PC2 axis, with few species scattered to the higher-value end of the PC1.

The PCA scores extracted from the PC1 and PC2 axis were reintroduced into the Aves sub-dataset. Then they were used to plot the scatter plot(Fig 2b) and create a linear model. The model suggested that the PC1 axis has a significant impact on the annual reproductive output ($p<0.001$), but PC2 has a weak and insignificant impact on the annual reproductive output ($p = 0.0672$).

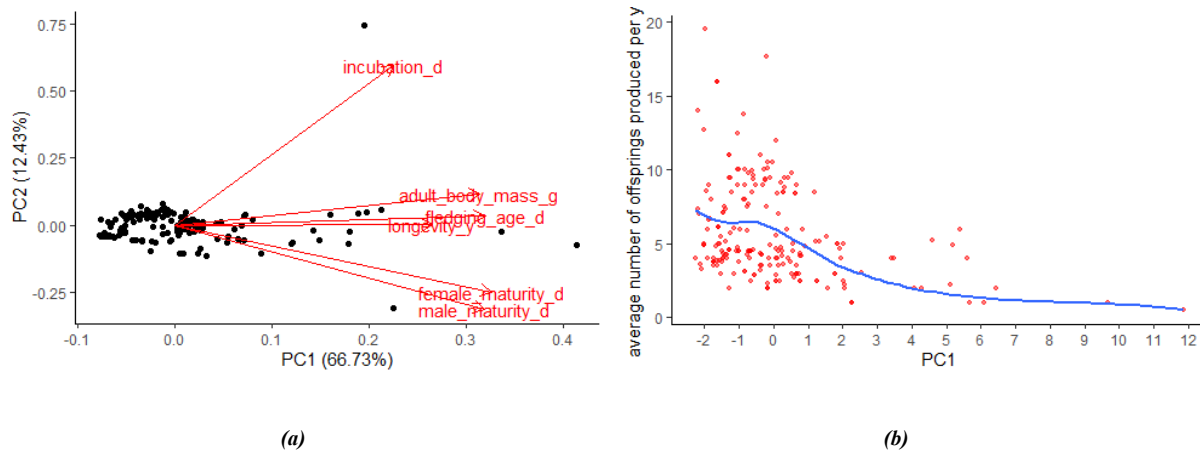*(a)*   *(b)*

Figure 2. (a) The result of Aves PCA. The combination of PC1 and PC2 explains 79.2% of variances. Each black dot represents a bird species, and red arrows represent the loadings of each trait. Based on the plot, the body mass, fledgling age, longevity, and time to maturity are positively correlated to PC1, and incubation time alone is positively correlated to PC2. (b) the result of the PCA model, the x-axis is the PC1, and the y-axis is the annual reproductive output. There is a negative relationship between the PC1 and the annual reproductive output. The scatter plot of PC2 was not shown since PC2 has no significant impact on the response variable.

2. Mammalia

The results from the correlation test of the class Mammalia revealed that many parameters are correlated to each other (Fig 3). Adult body mass is highly correlated to adult svl, birth weight, birth svl, and weaning weight, among all these parameters, adult body mass was selected as the representative.

```
Call:corr.test(x = mammal_avg_bodysize[, 6:16], method = "pearson")
Correlation matrix
                          adult_body_mass_g longevity_y litter_or_clutch_size_n adult_svl_cm birth_or_hatching_weight_g
adult_body_mass_g                      1.00        0.54                   -0.14         0.85                       0.91
longevity_y                            0.54        1.00                   -0.52         0.79                       0.69
litter_or_clutch_size_n               -0.14       -0.52                    1.00        -0.24                      -0.18
adult_svl_cm                           0.85        0.79                   -0.24         1.00                       0.95
birth_or_hatching_weight_g             0.91        0.69                   -0.18         0.95                       1.00
birth_or_hatching_svl_cm               0.82        0.80                   -0.26         0.98                       0.95
litters_or_clutches_per_y             -0.18       -0.61                    0.60        -0.34                      -0.25
gestation_d                            0.30        0.82                   -0.49         0.61                       0.42
weaning_d                              0.16        0.64                   -0.29         0.44                       0.23
weaning_weight_g                       0.98        0.61                   -0.16         0.92                       0.95
female_maturity_d                      0.34        0.88                   -0.40         0.70                       0.51
                          birth_or_hatching_svl_cm litters_or_clutches_per_y gestation_d weaning_d weaning_weight_g
adult_body_mass_g                             0.82                     -0.18        0.30      0.16             0.98
longevity_y                                   0.80                     -0.61        0.82      0.64             0.61
litter_or_clutch_size_n                      -0.26                      0.60       -0.49     -0.29            -0.16
adult_svl_cm                                  0.98                     -0.34        0.61      0.44             0.92
birth_or_hatching_weight_g                    0.95                     -0.25        0.42      0.23             0.95
birth_or_hatching_svl_cm                      1.00                     -0.34        0.60      0.38             0.90
litters_or_clutches_per_y                    -0.34                      1.00       -0.57     -0.43            -0.22
gestation_d                                   0.60                     -0.57        1.00      0.86             0.36
weaning_d                                     0.38                     -0.43        0.86      1.00             0.19
weaning_weight_g                              0.90                     -0.22        0.36      0.19             1.00
female_maturity_d                             0.67                     -0.55        0.92      0.82             0.42
                          female_maturity_d
adult_body_mass_g                      0.34
longevity_y                            0.88
litter_or_clutch_size_n               -0.40
adult_svl_cm                           0.70
birth_or_hatching_weight_g             0.51
birth_or_hatching_svl_cm               0.67
litters_or_clutches_per_y             -0.55
gestation_d                            0.92
weaning_d                              0.82
weaning_weight_g                       0.42
female_maturity_d                      1.00
```

Figure 3. This image shows the result of the Mammalia correlation test. It shows that many parameters are heavily correlated to each other. The absolute value indicates the level of correlation, and the + or - sign represents the direction of the correlation.

In the Principle Component Analysis (PCA) of the Mammalia (Fig 4a), PC axis 1 and PC axis 2 captured 93.3% of all the variations of the Mammalia life-history traits., Adult svl, average longevity, time to reach maturity and weaning time are positively correlated to the PC1 axis; adult body mass alone is negatively correlated to the PC2 axis. Most Mammalia species are concentrated near the zero region of both the PC1 and PC2 axis, with few species scattered to the higher-value end of the PC1.

The PCA scores extracted from the PC1 and PC2 axis were reintroduced into the Mammalia sub-dataset. Then they were used to plot the scatter plot (Fig 4b) and create a linear model. The model suggested that the PC1 axis has a significant impact on the annual reproductive output ($p < 0.001$), but PC2 has a weak and insignificant impact on the annual reproductive output ($p = 0.0619$).

(a)   (b)
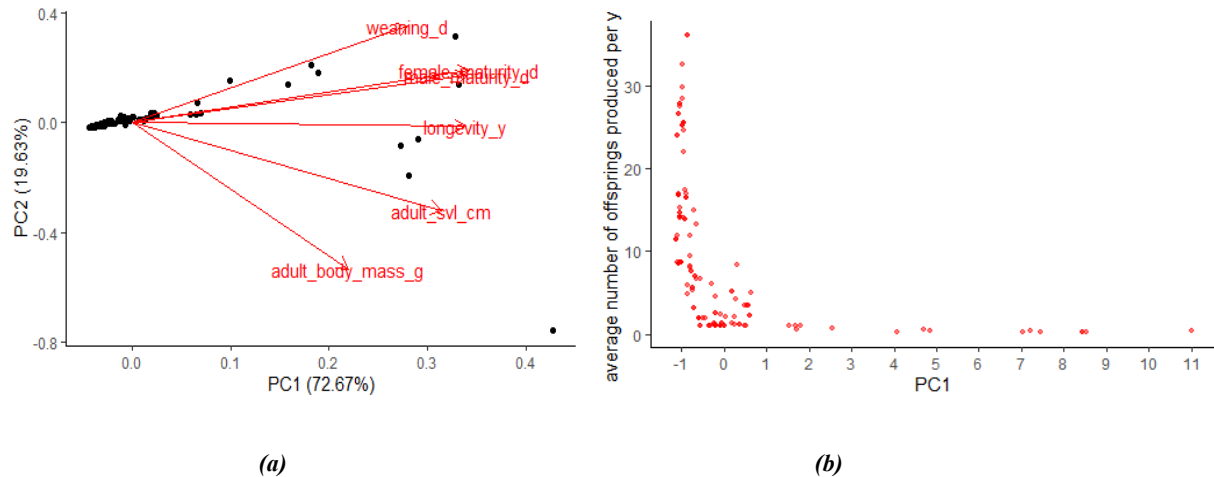
Figure 4. (a) The result of Aves PCA. The combination of PC1 and PC2 explains 93.3% of variances. Each black dot represents a mammal species, and red arrows represent the loadings of each trait. Adult svl, average longevity, time to reach maturity and weaning time are positively correlated to the PC1 axis; adult body mass alone is negatively correlated to the PC2 axis. (b) the result of the PCA model, the x-axis is the PC1, and the y-axis is the annual reproductive output. There is a negative relationship between the PC1 and the annual reproductive output. The scatter plot of PC2 was not shown since PC2 has no significant impact on the response variable.

3. Reptilia

Results from the correlation test of the class Reptilia revealed that many parameters are correlated to each other (Fig 5). Adult body mass is highly correlated to adult svl, egg mass and birth weight, among all these parameters, adult body mass was selected as the representative parameter.

```
Call:corr.test(x = reptile_avg_bodysize[, 6:15], method = "pearson")
Correlation matrix
                          adult_body_mass_g longevity_y litter_or_clutch_size_n adult_svl_cm egg_mass_g litters_or_clutches_per_y
adult_body_mass_g                      1.00        0.29                    0.34         0.81       0.96                     -0.23
longevity_y                            0.29        1.00                    0.17         0.39       0.41                     -0.23
litter_or_clutch_size_n                0.34        0.17                    1.00         0.73       0.44                     -0.56
adult_svl_cm                           0.81        0.39                    0.73         1.00       0.87                     -0.50
egg_mass_g                             0.96        0.41                    0.44         0.87       1.00                     -0.33
litters_or_clutches_per_y             -0.23       -0.23                   -0.56        -0.50      -0.33                      1.00
female_maturity_d                      0.61        0.48                    0.55         0.75       0.75                     -0.60
male_maturity_d                        0.66        0.38                    0.53         0.74       0.78                     -0.60
birth_or_hatching_weight_g             0.95        0.43                    0.51         0.90       0.99                     -0.36
incubation_d                           0.49        0.24                    0.61         0.83       0.59                     -0.40
                          female_maturity_d male_maturity_d birth_or_hatching_weight_g incubation_d
adult_body_mass_g                      0.61            0.66                       0.95         0.49
longevity_y                            0.48            0.38                       0.43         0.24
litter_or_clutch_size_n                0.55            0.53                       0.51         0.61
adult_svl_cm                           0.75            0.74                       0.90         0.83
egg_mass_g                             0.75            0.78                       0.99         0.59
litters_or_clutches_per_y             -0.60           -0.60                      -0.36        -0.40
female_maturity_d                      1.00            0.94                       0.78         0.55
male_maturity_d                        0.94            1.00                       0.81         0.45
birth_or_hatching_weight_g             0.78            0.81                       1.00         0.62
incubation_d                           0.55            0.45                       0.62         1.00
```

Figure 5. This image shows the result of the Reptilia correlation test. It shows that many parameters are heavily correlated to each other. The absolute value indicates the level of correlation, and the + or - sign represents the direction of the correlation.

In the Principle Component Analysis (PCA) of the Reptilia (Fig 6a), PC axis 1 and PC axis 2 captured 78.3 % of all the variations of the Reptilia life-history traits. Adult body mass, incubation time and time to reach maturity are positively correlated to the PC1 axis; average

longevity alone is negatively correlated to the PC2 axis. Most Reptilia species are scattered around the PC1 axis and concentrated near the zero of the PC2 axis.

The PCA score extracted from the PC1 and PC2 axis were reintroduced into the Reptilia sub-dataset. Then they were used to plot the scatter plot (Fig 6b) and create a linear model. The model suggested that the PC1 axis has an insignificant impact on the annual reproductive output (p = 0.072), but PC2 significantly impacts the annual reproductive output (p = 0.004).

(a)   (b)
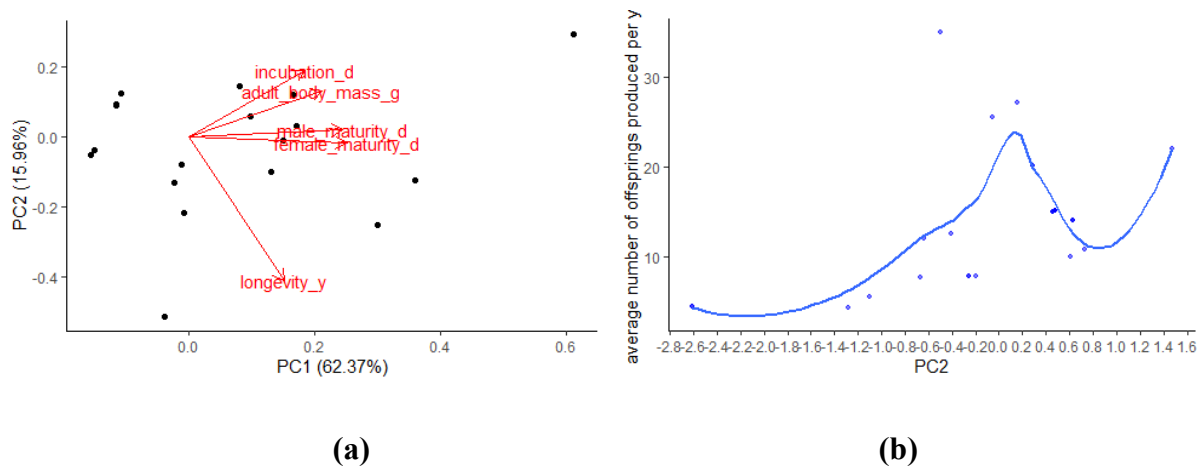
Figure 6. *(a) The result of Reptilia PCA. The combination of PC1 and PC2 explains 78.3% of variances in reptile life-history traits. Each black dot represents a reptile species, and red arrows represent the loadings of each trait. Adult body mass, incubation time and time to maturity are positively correlated to the PC1 axis; average longevity alone is negatively correlated to the PC2 axis. (b) the result of the PCA model, the x-axis is the PC2, and the y-axis is the annual reproductive output. There is a positive relationship between the PC2 and the annual reproductive output. The scatter plot of PC1 was not shown since PC1 has no significant impact on the response variable.*

Discussion

Our results show that all traits examined have a negative correlation with reproductive rate with some variation between birds, mammals and reptiles. Specifically, the PC1 axis was found to be significantly negatively correlated (p $= 2 * 10^{-16}$) with reproductive output in mammals and birds as shown in figures 2b and 4b. Since all traits examined contributed a moderate amount to the PC1 axis and all vary togather, we conclude that these traits have a negative correlation with reproductive output in mammals and birds. Results also showed a minor correlation between the PC2 axis and reproductive rate for birds and mammals but these results were not significant (p > 0.05 for Aves and Mammalia). However, the PC2 axis was found to be significantly positively correlated (p = 0.005) with reproductive rate in reptiles as shown in figure 6b. In Reptilia, longevity contributed the most to the PC2 axis with all other traits contributing little to the axis. Since longevity contributed negatively to the PC2 axis and PC2 was significantly positively correlated to reproductive output, longevity was determined to be

negatively correlated with reproductive rate in reptiles. Furthermore the PC1 axis showed a minor correlation (p-value = 0.08) with reproductive rate in reptiles but this correlation was not as significant as the PC2 axis.

All developmental traits showed a negative correlation to reproductive output in birds and mammals with longevity also being negatively correlated in reptiles. Based on this we can reject the null hypothesis that reproductive output has no correlation with developmental traits. Furthermore these results support the alternative hypothesis that reproductive output correlates with developmental traits. These results also support our prediction that developmental traits will be negatively correlated with reproductive output across all classes, although only longevity was significantly correlated in reptiles. This makes sense based on life history theory as well as current literature as species with high values for these traits (longevity, mass, maturity time, ect.) will generally produce less offspring per year as they invest more resources into making sure the offspring they do produce develop to sexual maturity (Walker et al. 2007).

Studies have shown that species with low reproductive rate are more sensitive to habitat loss (Quesnelle et al. 2014), but despite this IUCN still uses population metrics as their only method for determining species extinction risk (IUCN ,2022). Since our results determined that developmental traits are negatively correlated with reproductive rate, we can conclude that species with high values for these traits would also be more sensitive to habitat loss. Therefore, by using these traits we would be able to determine how at risk a species may be in a more accurate manner than population metrics alone would dictate. In other words, by knowing that developmental traits are negatively correlated with reproductive rate they can then be used in conjunction with population metrics to more accurately determine a species extinction risk.

Limitations and Future Work

The data was gathered from a large variety of sources. It's hard to imagine that all those sources used similar data gathering methods. As a result, there are probably biases introduced into the dataset by those varying sampling methods but given the large size of the dataset (36 columns and more than 21300 rows) and the vast amount of sources the author cited (more than 1000 sources cited), it's unlikely that any of the biases would be consistent across the entire dataset. Due to this it is likely that bias was minimized in this analysis.

The main limitation in our dataset was the limited amount of data present for certain traits. Traits in our dataset varied greatly in the amount of N/A values present. Due to this some traits had to be excluded in our analysis. The Reptilia class in particular was affected by this as after removing NA values only 32 data points remained compared to 206 and 152 in Aves and Mammalia respectively. This discrepancy could potentially explain why the results for reptiles

differed from birds and mammals. In other words, some of the traits determined to be insignificant in reptiles may have been found to be significant if more data was available.

Two avenues that future work could focus on would be to examine a wider variety of traits or to examine differences within each class as opposed to differences between them. First, a wider range of traits could be examined. Some traits in the dataset contained little to no data and therefore adding more traits into our analysis, or even more data for the traits already analysed may produce better results. Moreover, other classes could also potentially be looked at as our analysis only considered mammals, birds and reptiles. Furthermore, differences within each class could also be looked at. For example, the differences between raptors (Accipitriformes) and waterfowl (Anseriformes) may be more important in conservation efforts than the difference among birds and reptiles.

Life history traits related to size, maturity, and longevity were found to be negatively correlated to reproductive output in birds and mammals with only longevity being correlated in reptiles. This is expected under life history theory and suggests that species with large values for these traits will be more susceptible to habitat loss and therefore should be a higher priority in conservation efforts. Despite this, additional analysis can still be done to further identify which groups of species may be at risk.

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Supplementary Materials

Data and code required to reproduce analysis can be found on github.