The Comparative Method:
The Importance of Controlling for Phylogeny in the Study of Seabird Breeding Biology

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Abstract

Interspecific comparative biological analysis has undergone a fundamental change over the past two decades in order to account for phylogenetic relationships between species. Traditionally, comparative methods have incorporated the simplifying assumption that species are independent, when in fact, biological groups are related differentially depending on their unique phylogenetic history (Felsenstein 1985, Mahler 2002). Comparative methods have been widely utilized to infer evolutionary adaptation and it is believed that the incorporation of phylogenetic information can increase both the quality and the type of inference possible from comparative data (Garland 2005). Here I investigate the importance of controlling for phylogeny in the comparative analysis of seabird life history traits. I examine the effects of phylogenetic correction on the correlation between traits. My findings demonstrated that the failure to correct for phylogenetic history affects the outcome of statistical analysis in two ways. First it can influence the relative strength of reported correlations even when a significant relationship is detected by both methods. Second, when phylogeny is important to an apparent correlation, the likelihood of conducting a Type I error is increased and these falsely detected correlations can be avoided by accounting for phylogeny in statistical methodology. Results from this study suggest that controlling for phylogenetic relationships is important when conducting comparative studies between related species groups.

Introduction

The utilization of species comparisons to test hypotheses concerning adaptations is one of evolutionary biology's most enduring traditions. Charles Darwin utilized such comparisons as evidence for his theory of evolution by natural selection (Darwin 1859). In modern times, interspecific comparisons are fundamental to many fields of biology. Behavioral ecology, comparative physiology, community ecology, functional morphology, comparative biomechanics and the study of sexual selection all rely on comparative analysis to test hypotheses within their fields. The comparative method has become widely utilized because it allows for the use of information pertaining to a large number of species-specific variables to be analyzed without imposing manipulative studies on the species under observation. The comparative method can involve looking for correlations between characters belonging to different species or members of higher taxa (Felsenstein 1985). It can be used to tease apart what traits are adaptations to what circumstances (Noy-Meir 1970) and to provide evidence for adaptation through the utilization of patterns in the interspecific evolution of correlated traits (Pagel 1999). Evaluating these relationships is a useful means of understanding the basic ecology and evolutionary patterns evident in different species. Comparative analysis allows us to estimate the influence one trait has on another and allows for the estimation of life history trait values for species where little information is available.

Relationships between life history traits can be evaluated using a range of comparative methods, each with its own set of assumptions, strengths and weaknesses. For example, traditional comparative analysis has relied on conventional statistical methods to test for correlations between life history traits and between traits and environmental variables. This methodology treats all data as statistically independent. The assumption of independent distribution of characters among species would be justified if the evolution of each lineage were independent of the others and if character changes were derived from a bivariate normal distribution; however, species are invariably related to one another to a greater or lesser extent based on their evolutionary history (Felsenstein 1985). The failure to account for phylogeny in cross-species comparisons leads to a range of statistical errors including an overestimation of the strength of significance and an increased likelihood of obtaining a Type I error because the estimated number of independent observations is too high (Felsenstein 1985, Harvey and Mace 1982, Baker and Parker 1979). The problem of

non-independence has not gone unnoticed in past comparative studies. In fact, techniques like nested analysis of variance to find taxonomic level and the use of genus-level, rather than species-level, comparisons have been implemented to account for much of the error inherent in traditional methodologies (Clutton-Brock and Harvey 1977). However, these methods do not allow for analysis on the species level and do not fully account for phylogeny, limiting their application and usefulness in comparative analysis (Gittleman and Kot 1990).

With a known phylogeny and a model of evolutionary change, it should be possible to correct for the non-independence of taxa (Felsenstein, 1985). In fact, statistical methods in which phylogeny and evolutionary dynamics are directly incorporated into the statistical design have been developed in the last two decades. This is, in part, due to the increasing availability of reliable phylogenies (Pagel, 1997) and the design of statistics packages that incorporate phylogeny (Garland, 2005). With recent advances in the study of the comparative methodology, implementation of a phylogenetically informed analytical method can increase statistical power and thereby detect relationships among traits (Harvey and Pagel, 1991; Garland, 1992; Garland, 2005). These phylogenetically informed models allow for comparisons to be conducted on the species level without the problems associated with traditional statistical methodologies (Gittleman and Kot, 1990). As the use of phylogenetically corrected methodologies becomes more commonplace in biological studies, the question of how its application will affect the outcome of past and present analyses has become increasingly relevant (Rheindt et. al., 2004).

Birds provide an excellent group for comparative analysis, and they have been the subject of many comparative studies. This is due largely to the immense body of literature available regarding avian natural history and taxonomy. For at least two centuries both professional and amateur ornithologists have been collecting information on avian life history traits. As a result, birds are exceptionally well studied compared to other vertebrates and have acted as the foundation for a large range of ecological, behavioral, and evolutionary theories (Bennett and Owens, 2002). However, relatively few of these comparative studies on birds have been conducted on the species level in a manner that corrects for phylogenetic

relatedness. Thus data on birds may be especially good for assessing the outcome of incorporating phylogeny into comparative methodologies.

For the purposes of this paper I have chosen to focus on seabird breeding biology. I have selected this group for three primary reasons. 1) Like land birds, seabirds have been extensively studied on the species level, allowing for the compilation of ample data to assess correlations between a variety of traits (Gaston, 2004; Croxall, 1987). 2) Phylogenies based on reliable methodologies are available for a range of seabird species (Austin, 1996; Kennedy and Page, 2002). 3) Seabirds have many life history characteristics that are different from those of terrestrial birds (Croxall, 1987). They rely on patchy and ephemeral food sources and forage in habitats that are quite different from their breeding habitats (Finkelstein and Keitt, in prep.). These environmental parameters have lead to the evolution of a unique suite of characteristics in seabirds. The combination of these three factors makes seabird breeding biology an interesting subject for comparative analysis and provides for a manageable data set for investigating the importance of controlling for phylogeny in the comparative analysis of seabird life history traits.

Previous studies on seabird breeding biology that have not taken phylogeny into account have found positive correlations between a wide range of life history traits, including female mass and egg incubation period, egg mass and fledging period (Finkelstein and Keitt, in prep.; Hammer et al., 2002, pg. 217) and between fledging period and both age of first breeding and egg mass (Boersma, 1982; Rahn et al., 1974). Studies that have incorporated phylogeny show no direct correlation between female mass and incubation period or age of first breeding in birds (Bennett and Owens, 2002). It is my intention to test these relationships and to show the impact of incorporating phylogenetic relatedness into correlational analyses on a subset of marine bird life history traits. I expect that the incorporation of phylogeny will result in significantly different correlations than are revealed by traditional methodologies. If this assertion is supported, comparative analyses of some traits should correlate regardless of methodology, while others that are significant using traditional statistics will not be significant when phylogeny is taken into account. This is due to a type I error in the traditional statistics. It is also possible that correlations between traits confounded by the assumptions inherent in traditional methodologies will be significant

when phylogeny is accounted for. This is due to the increased power of using a phylogenetically informed method.

Methods

Database Development

Working with Myra Finkelstein and Brad Keitt, I compiled a database of 330 seabird species, taking into account 19 of their life history traits. The database includes the common names, genus, species and family for each marine bird and their associated life history traits: age of first breeding, breeding region, nest type, egg mass, clutch size, incubation period, hatch state, chick mass at hatch, maximum chick mass, maximum chick mass as a percent of adult mass, fledging period, adult mass, wing chord, wing span, mean wing loading, wing aspect ratio, foraging distance, and threat status. I reviewed scholarly papers using electronic search engines, including BIOSIS, Web of Science, and BNA, and I searched the libraries of Yale University, the University of California at Santa Cruz, and the University of California at Berkeley. Searches were used alone and in combination to locate scientific literature, and the data cited was traced to the most original source available. Key words included seabirds, marine birds, scientific and common names for the 330 species, and each of the 19 life history traits.

Due to the inevitable differences in field methods, data collection, and data presentation in biological studies, one of the major challenges of this type of analysis is the data compilation. For this reason, I chose each set of data based on specific guidelines. To avoid biasing measurements, I did not average data from different bird colonies. Instead, when multiple values were available from various locations, I recorded the data from the published studies with the largest sample size. This was intended to limit the incorporation of artifacts common when sample size is smaller. I included both male and female masses to account for sexual dimorphism and used average mass when appropriate. From this database I selected a subset of life history traits with continuous data to conduct comparisons between statistical methods.

Statistical and Phylogenetic Analysis

Two statistical packages were implemented in this study. 1) I conducted traditional, nonphylogenetically corrected, least squares regressions using SYSTAT. 2) I implemented the PDAP module (Midford et. al., 2005) in the program MESQUITE (Maddison and Maddison, 2006) to run least squares regressions using two phylogenies. The analyses were

restricted to five life history traits selected from the database. These included: female mass, egg mass, incubation period, fledging period and age of first breeding.

I incorporated two separate phylogenies in my analysis. One, a polytomy (Appendix B), was used to mimic traditional statistical tests in which phylogeny is not accounted for. A polytomy is equivalent to an unresolved phylogenetic tree, and assumes that all species are equally related. Results from a regression analysis run using this polytomy in MESQUITE was run and found to be equivalent to the analysis run in SYSTAT. (The polytomy was utilized to illustrate this equivalence with traditional statistics, and to verify that the data entered in the PDAP program was being analyzed correctly.) The second phylogeny was fully resolved (Appendix A) and shows the descent of each species as it relates to every other species. This fully resolved phylogeny allowed for the incorporation of species relatedness into the statistical analysis, thus accounting for phylogeny in a manner neither of the other methods were capable of accomplishing.

I based the resolved phylogeny on a seabird supertree from Kennedy and Page (2002). Species whose branches could be traced back to unresolved nodes were either eliminated from the phylogeny or resolved using phylogenies from Austin (1996). The data used to examine the relationships among species in these phylogenies came from partial mitochondrial cytochrome *b* gene sequences. As branch lengths for all 123 species were not available, I set all branch lengths to 1 (Garland and Ives, 2000). I checked the standardization of branch lengths and found all five life history traits to be within an acceptable range (Maddison, 1995). I log transformed the data to normalize the contrasts used in both programs. This was important in order to compare results between methodologies.

Results

The least squares regression results from SYSTAT and the MESQUITE polytomy showed little to no variation, while the resolved MESQUITE phylogeny resulted in unique values for the correlations evaluated. I found a significant correlational difference between methodologies in four out of ten regression analyses. The remaining six regressions showed marked reductions in the strength of the correlations being analyzed. (Appendix C).

Egg mass vs. female mass and age of first breeding

Both traditional statistical methods and the phylogenetically informed method showed egg mass to positively correlate with female mass (r^2= 0.88, $p<0.05$ and r^2=0.77, $p<0.05$). This suggests that once phylogeny is accounted for, approximately 77% of the variation in egg mass between species is explained by the mass of the female bird. Egg mass and age of first breeding, on the other hand, did not show a significant relationship when phylogeny was accounted for ($p=0.06$) even though the analysis run in SYSTAT and using the polytomy suggested it did (r^2=0.22, $p=0.002$).

Age of first breeding vs. female mass and fledging period

Age of first breeding was found to correlate with female mass using traditional statistics (r^2=0.87, $p=0.02$), but this relationship was not found to be significant using the resolved polytomy ($p=0.49$). Age of first breeding and fledging period were found to correlate using both methodologies, but the relative signal was different depending on the method used. When phylogeny was not accounted for, the relationship appears to be much higher (r^2=0.27, $p<0.05$) than when phylogeny was incorporated (r^2=0.02, $p=0.03$).

Incubation period vs. egg mass, female mass and age of first breeding

Incubation period was found to correlate with egg mass both when phylogeny is not incorporated (r^2=0.24, $p<0.05$) and when it is (r^2=0.017, $p=0.002$). The small change in interaction strength shows phylogeny to play a smaller role in the correlation between these two variables than it does in other relationships. On the other hand, incubation period was found to correlate with female mass (r^2=0.088, $p=0.004$) and age of first breeding (r^2=0.13,

p=0.005) using traditional statistics, but the incorporation of phylogenetic relationships did not support these results (p=0.13 and 0.61, respectively).

Fledging period vs. female mass, egg mass and incubation period

Regardless of methodology, fledging period was found to correlate with female mass, egg mass and incubation period. The incorporation of phylogeny impacted the strength of the correlation in all three cases. By accounting for the relationships among species, the correlation between fledging period and female mass was reduced from 43% to 28% (r^2=0.43, $p<0.05$ and r^2=0.28, $p<0.05$, respectively) and the relationship between fledging period and egg mass was reduced from 47% to 29% (r^2=0.47, $p<0.05$ and r^2=0.29, $p<0.05$). Furthermore, the relationship found for incubation period and fledging period was reduced from 19% to 6% when phylogeny was accounted for (r^2=0.19, $p<0.05$ and r^2=0.066, p=0.01)

Discussion

My results show the utility of using phylogenetically corrected comparisons among species rather than using traditional statistics that do not account for phylogeny. In this paper I have worked to demonstrate the strengths of performing an analysis that has incorporated phylogenetic information. Failure to correct for phylogenetic history can affect the outcome of statistical analysis in two fundamental ways: 1) the relative strength of reported correlations often differs even when both phylogenetic and non-phylogenetic analysis agree as to significance, and 2) the risk of conducting a Type I error is greatly diminished by the incorporation of phylogeny.

Of the ten regressions analyzed, eight reinforced the findings of recent phylogenetically based comparative analysis of all marine and terrestrial bird families conducted by Bennet and Owens (2002, p 43) (Figures 1 and 2).

Correlations Documented in This Study: Based on Resolved Phylogenies of Seabirds	**Previously Documented Correlations:** Based on Resolved Phylogenies of Ancient Avian Lineages
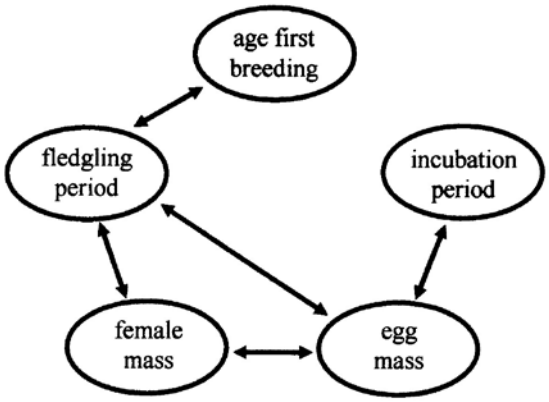	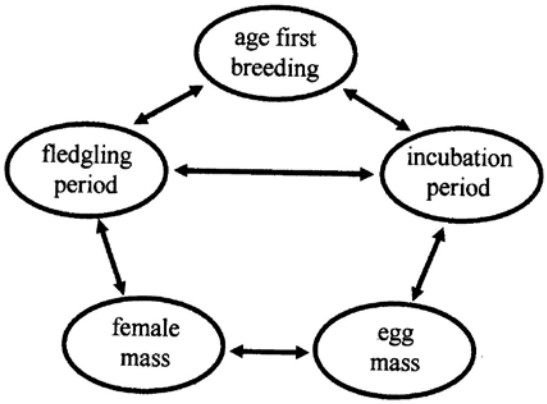
Figure 1: Core life history relationships from phylogenetically based regressions on seabirds. Arrows indicate the presence of significant correlations between life history traits.	**Figure 2:** Core life history relationships from phylogenetically based regressions among ancient avian lineages (families and orders) from Bennet and Owens (2002, p 43). Arrows indicate the presence of significant correlations between life history traits.

However, whereas they found no significant relationship between egg weight and fledging period, my analysis shows a positive correlation between these two traits, suggesting that egg mass has a 29% impact on the fledging period of chicks. Furthermore, whereas they found a positive correlation between incubation period and age of first breeding, I found no

significant relationship. This incongruence may be due to a number of factors. Bennet and Owens looked at terrestrial and marine species on the family level, so the difference in correlations may be an indication of the unique adaptations of seabirds as compared to terrestrial species. Alternately, it may be the result of differences in the phylogenies used or the scale of the analyses. This study was conducted on the species level and as a result it may resolve relationships that cannot be resolved on the family level.

A more inclusive study of seabird life history traits would have been possible with the availability of a more complete supertree for marine bird species. In this analysis I was capable of evaluating 124 out of 330 seabird species from my database (Appendix A). Furthermore, the branch lengths for each species were assigned a length of one. This arbitrary length does not reflect the differing divergence times for each species and thus does not fully reflect the evolutionary history of seabirds. However, previous studies have shown that the use of arbitrary branch lengths has little to no effect on results in comparative analyses (Rheindt et. al., 2004). Although the analysis of seabird life history traits might have been improved by the analysis of a greater number of species, my analysis of different comparative methods was not limited by the number of species included, and branch lengths were not likely to affect the phylogenetic analysis.

It was evident in six of the ten compared regressions that the inclusion of phylogenetic relationships can influence the relative strength of reported correlations, even when significant relationships are detected by both phylogenetically informed methodologies and traditional nonphylogenetic methods. For example, the regressions run for fledging period and female mass suggested that 43% of the variation in egg mass across species was due to the influence of female body mass, but the incorporation of phylogeny brought this down to 28% ($P < 0.05$). These overestimations demonstrate that although the influence of phylogeny can sometimes be subtle, it can also have a relatively large impact on the strength of correlations.

Four out of ten of the regressions preformed resulted in correlations that appear significant using nonphylogenetic methods and not significant with the incorporation of the species phylogeny (Figures 3 and 4). This discrepancy could be the result of low power in the phylogenetic analysis (Type II error), but this is unlikely as the sample sizes used were relatively large (Harmon and Losos, 2005). More likely, the significant values resulting from

traditional methodologies were due to an overestimation of the independence of species, a Type I error (Felsenstein, 1985; Harvey and Mace, 1982; Baker and Parker, 1979). My results suggest the importance of controlling for phylogenetic relationships when conducting comparative studies and further reinforce the idea that the incorporation of independent estimates of phylogenetic relationships can increase statistical power to detect relationships. This increase in power can also decrease the likelihood of conducting Type I errors.

Correlations Documented in This Study: Based on Non-Phylogenetic Analyses of Seabirds	**Correlations Documented in This Study:** Based on Phylogenetic Analyses of Seabirds
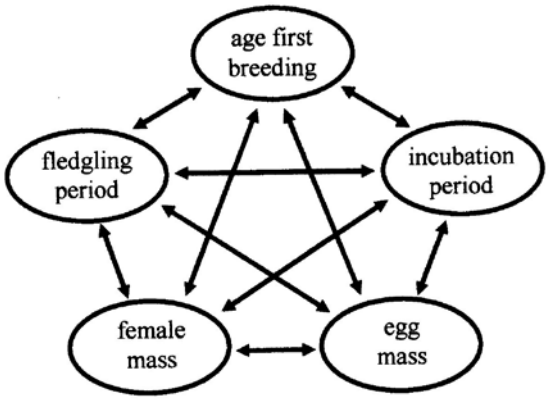	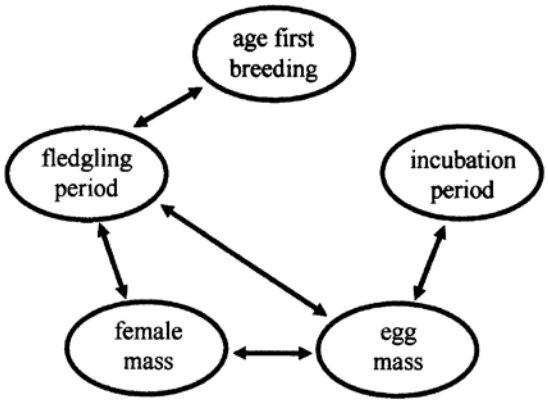
Figure 3: Core life history relationships among seabirds from regression analysis not corrected for phylogeny. Arrows indicate the presence of significant correlations between life history traits.	**Figure 4:** Core life history relationships among seabirds from phylogenetically based regressions. Arrows indicate the presence of significant correlations between life history traits.

As is evident in Figures 3 and 4, nonphylogenetic regression results differ substantially when compared to those of phylogenetically corrected methodologies. In four out of ten regression analyses, I found significant correlational differences between methodologies. The remaining six regressions showed marked reductions in correlational strength. This is likely due to evolutionary relatedness resulting in an apparent correlation between traits due to shared evolutionary history, which tend to increase the apparent strength of the correlation analyzed by traditional statistics. These results suggest that future studies regarding seabird life history traits would be improved by the incorporation of seabird phylogenies, because many of their life history traits are significantly correlated with their phylogenetic histories.

Understanding the basic ecology and evolutionary patterns of different species relies on sound statistical methodologies. With recent advances in the study of the comparative methodology, the implementation of a phylogenetically informed analytical method provides the opportunity to reassess many of our longstanding views of life history traits and adaptive patterns (Pagel, 1997). It also allows us to correct past assumptions embedded in our statistical methodologies that may lead to skewed or inaccurate results in comparative analysis (Felsenstein, 1985; Garland, 2005; Harmon and Losos, 2005). Statistical modeling techniques that accurately reflect the relationships between life history traits are still being developed (Pagel, 1999), but as this and other studies demonstrate, the application of comparative methods based on resolved phylogenies and statistically informed models can improve our understanding of diversity and patterns of adaptation observable in nature.

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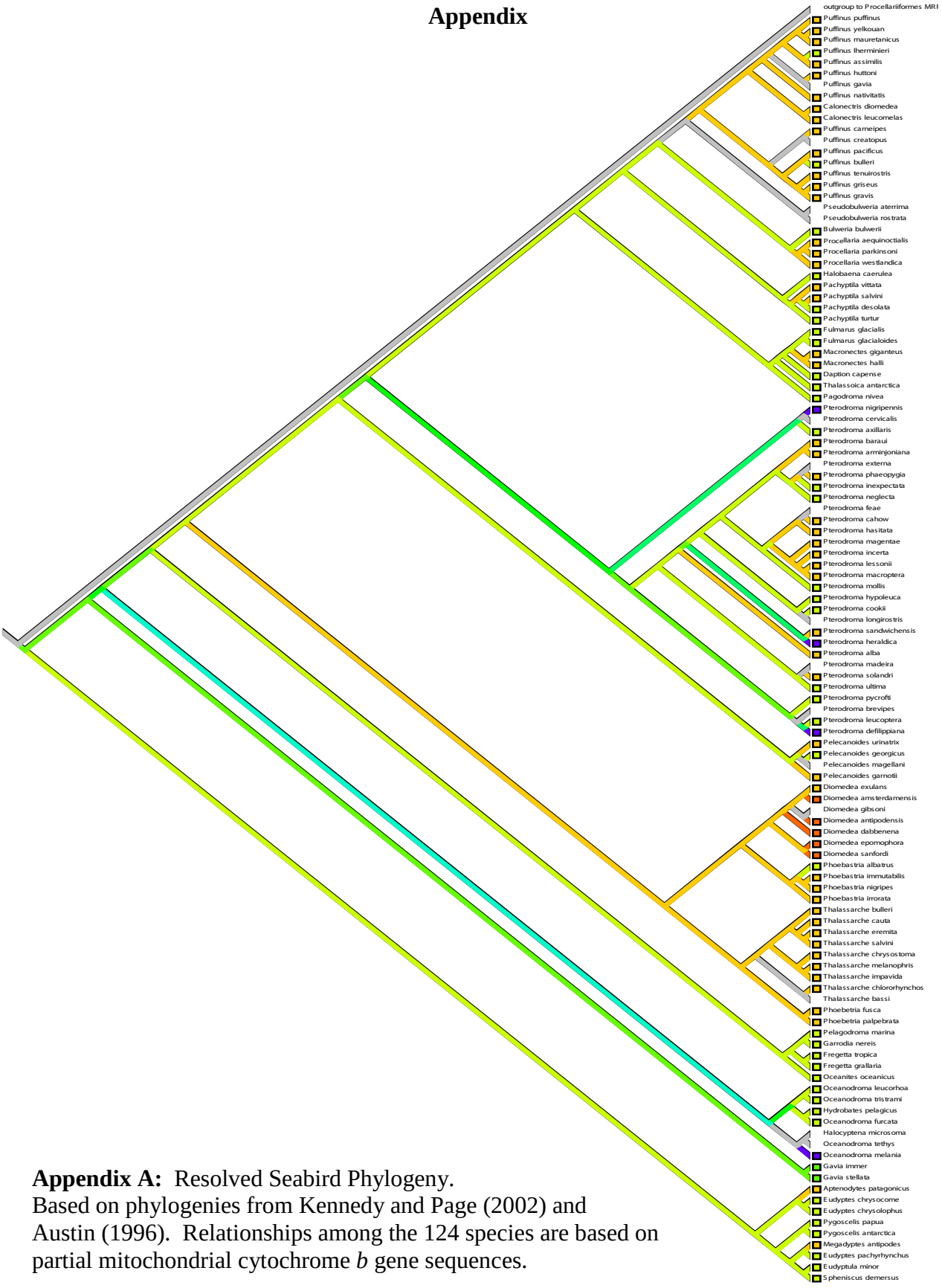
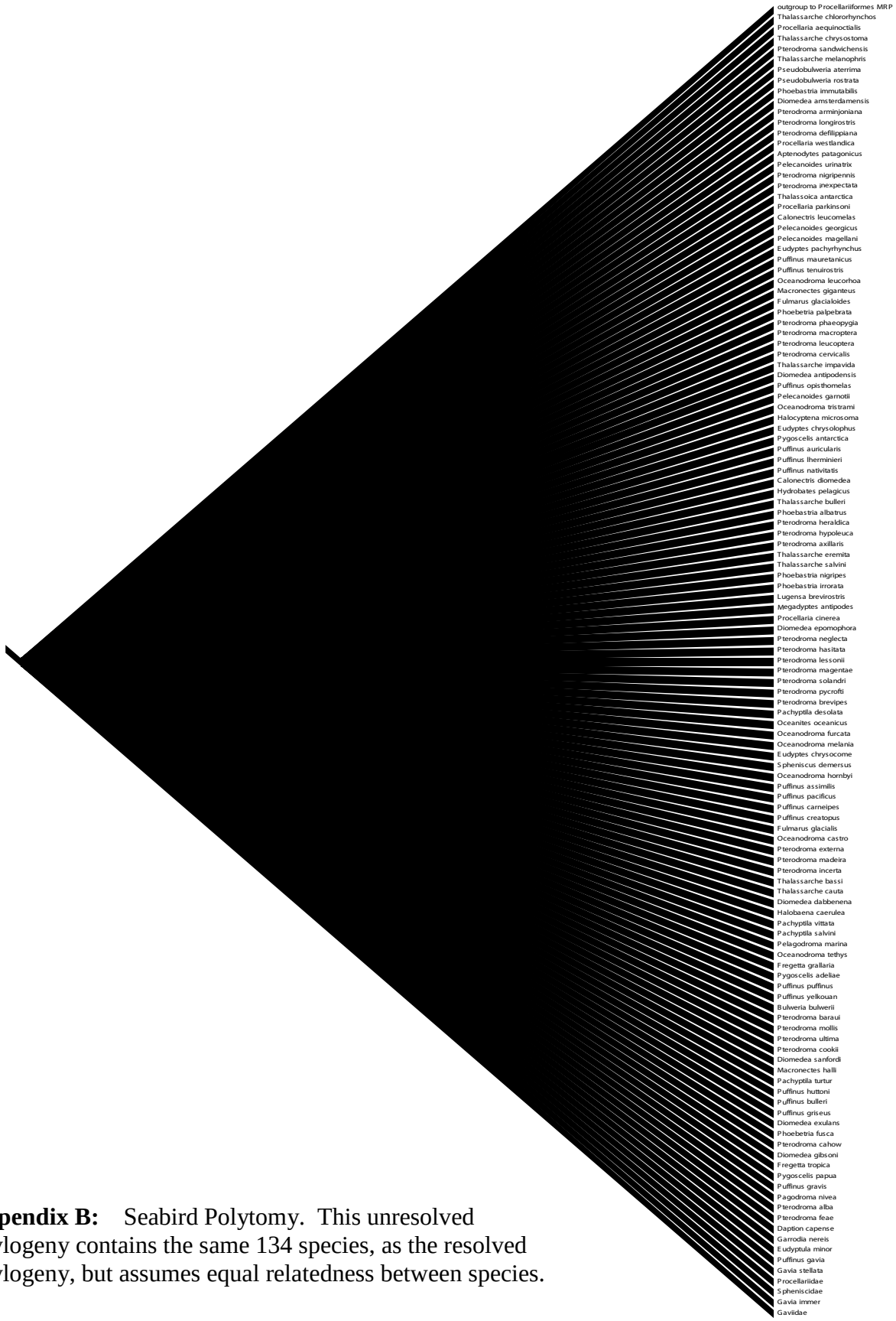
Appendix



Appendix A: Resolved Seabird Phylogeny.
Based on phylogenies from Kennedy and Page (2002) and Austin (1996). Relationships among the 124 species are based on partial mitochondrial cytochrome *b* gene sequences.



Appendix B: Seabird Polytomy. This unresolved phylogeny contains the same 134 species, as the resolved phylogeny, but assumes equal relatedness between species.

Least Squares Regression Results

Dependent Variable (Y)	Independent Variable (X)	SYSTAT				MESQUITE POLYTOMY				MESQUITE RESOVED			
		r^2	P	Slope	Contrast Number	r^2	P	Slope	Contrast Number	r^2	P	Slope	Contrast Number
Log Egg Mass	Log Female Mass	0.88	***	0.642	50	0.88	***	0.64	49	0.77	***	0.62	49
Log Age of First Breeding	**Log Female Mass**	**0.087**	**0.02**	**0.088**	**59**	**0.09**	**0.02**	**0.09**	**58**	**0.008**	**0.49 NS**	**0.042**	**58**
Log Incubation Period	Log Egg Mass	0.24	***	0.099	53	0.24	***	0.10	52	0.17	0.002	0.12	52
Log Incubation Period	**Log Female Mass**	**0.088**	**0.004**	**1.139**	**92**	**0.09**	**0.004**	**1.14**	**91**	**0.02**	**0.13 NS**	**0.16**	**91**
Log Fledgling Period	Log Female Mass	0.425	***	0.179	91	0.43	***	0.18	90	0.28	***	0.21	90
Log Age of First Breeding	Log Fledgling Period	0.268	***	0.50	61	0.27	***	0.50	60	0.02	0.03	0.16	60
Log Fledging Period	Log Egg Mass	0.471	***	0.274	53	0.47	***	0.27	52	0.29	***	0.32	52
Log Incubation Period	**Log Age of First Breeding**	**0.126**	**0.005**	**0.42**	**61**	**0.13**	**0.005**	**0.42**	**60**	**0.005**	**0.61 NS**	**0.08**	**60**
Log Incubation Period	Log Fledging Period	0.19	***	0.46	94	0.19	***	0.46	93	0.066	0.01	0.34	93
Log Egg Mass	**Log Age of First Breeding**	**0.22**	**0.002**	**1.02**	**39**	**0.22**	**0.002**	**1.02**	**38**	**0.10**	**0.06 NS**	**0.50**	**38**

Appendix C: Life History correlations among marine birds. *** indicate that P<<0.05. NS signifies results that are not significant. In bold I have highlighted the regressions that resulted in a significant difference between nonphylogenetic and phylogenetic analysis results. All other tests resulted in no significant difference between types of analysis.

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