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Trait Evolution in Anseriformes: Is Evolution of Body Mass, Diet, Locomotory Behavior, and Diel Activity Pattern Correlated?

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Trait evolution in Anseriformes: is evolution of body mass, diet, locomotory behavior, and diel activity pattern correlated?

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by

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Trait evolution in Anseriformes: is evolution of body mass, diet, locomotory behavior, and diel activity patterns correlated?

Abstract:

The morphologies and behaviors of animals evolve and diversify, filling ecological niches in their environments. In this study I examine how a morphological trait, body mass, and three ecological traits, namely diel activity patterns, diving/non-diving locomotion, and diet, evolve in the Anseriformes (waterfowl). Through ancestral state reconstructions using a maximum likelihood approach the evolution of these traits was compared to see if any patterns of trait coevolution emerged. Body mass was compared to each ecological trait using a phylogenetic ANOVA to test if there were body size differences between ecological groups. The pattern of male and female body mass evolution across the clade was found to be remarkably similar, indicating that selection effected body mass in similar ways between the sexes. Diving locomotion appears to be the ancestral state for Anseriformes with non-diving independently evolving probably five times. The ancestral state of diet appears to be either herbivory or omnivory, with carnivory secondarily evolving twice independently. For diel activity patterns, the ancestral state reconstruction showed little resolution at the internal nodes, indicating the high degree of plasticity in this trait among the species studied. Body mass in both males and females was not significantly correlated with any particular diet, diving locomotion, or diel activity pattern.

Introduction:

In this paper I examine the evolution of body mass, diet, locomotory behavior, and diel activity patterns in the Anseriformes (waterfowl), an ecologically diverse and speciose clade of birds. Specifically I seek to better understand possible correlation among trait evolution and aim to explore whether a morphological trait (body mass) and behavioral traits (diel activity pattern, diving/non-diving locomotion, and diet) coevolve. The study clade of Anseriformes includes ducks, geese, and swans, and data from living species in North America will be focused on in this study.

Species that are more closely related tend to share traits through common ancestry, and phylogenies provide a way to assess if traits co-vary evolutionarily (Nunn 2011).

Understanding if and how traits correlate and evolve together can shed insight on how species adapt to fill ecological niches. Phylogenies describe the hierarchical descent of species from a common ancestor. Through looking at the character states of contemporary species, it is possible that this information, when combined with the phylogeny, helps reconstructing historical events in evolution. One way to form hypotheses about trait evolution is to reconstruct a "painting" of how species evolved along the branches of the phylogeny (Pagel 1999). By mapping the character states of the contemporary Anseriformes on the phylogeny, we can begin to elucidate how these character states evolved.

Common wisdom holds that morphology and behavior are tightly linked in an evolutionary sense. Morphology may influence behaviors to a high degree, as it limits what an animal is physically capable of. Vice versa, some behaviors may also influence morphological evolution, because it imposes disparate physical constraints on the organism. It thus makes sense that various morphologies will impact what a species eats, how they move, and when they are active. Body size in particular appears to be related to ecological traits. For this reason, I will be looking at if and how body size relates to diet, diel activity patterns, and diving behavior across the Anseriformes. Diet is an important study trait, as it helps us understand the ways in which species adapt to and exploit the environments they live in, or how habitat influences the behavior of species (Johnsgard 2010). Locomotion is also an important indicator of how species adapt to exploit their environment, as there are energetic costs associated with different locomotor strategies (Johnsgard 2010). Diel activity patterns partially determine the visual environment of a species with regard to variable light conditions. This trait can help elucidate the relationship between ecology and morphologies, as different morphologies allow species to maximize their visual performance to the light conditions in which they occupy (Schmitz and Motani 2010).

My thesis is a first step towards a better understanding of possible co-evolutionary patterns in Anseriformes. I will first reconstruct the evolution of body mass and three ecological traits, and then test if there are body mass differences between waterfowl with different ecologies.

Materials and Methods:

Data collection

First, I obtained data about locomotory behavior, diet, and diel activity patterns from Birds of North America Online and *Waterfowl of North America* (Johnsgard 2010), and collected body mass data from *Handbook of Avian Body Masses* (Dunning 2008). The body masses were reported as average values for males and females separately, with values reported variably as seasonal or year-long averages (Dunning 2008). These data were then used to classify the traits of the species being studied into discrete categories. Diet was classified into carnivorous, omnivorous, or herbivorous. Species were classified into carnivorous or herbivorous if it was indicated that the species' diet was primarily comprised of animal/insect material or vegetation, and species were classified as omnivorous if both animal/insect and vegetation were commonly consumed. An omnivore might have a diet comprised of both plants and animals that are consumed regularly, like *Cygnus olor*, which eats submerged vascular plants, tadpoles, toads, mollusks, and insects (see Appendix). Alternatively a species may be classified as omnivorous if its diet changes seasonally to include both vegetation and animal material. For example, *Aythya valisineria* eats mainly plant material during the winter, but incorporates insects as a major food source during breeding season (see Appendix) When looking at locomotory activity, the concern was whether or not the species was known to dive or not. Species were classified as divers if they were observed diving for any reasons including food capture or to avoid predation and other threats. Diel activity patterns were classified as diurnal, nocturnal, or cathemeral, indicating day and night active species. Species were classified as diurnal if they primarily were observed feeding during the day, nocturnal if they were primarily observed feeding during the night, and cathemeral active if they were observed feeding during day and night, even if this changed seasonally, or if they fed during twilight hours. These classifications were similar to those used in other studies concerned with diel activity patterns, which classified species based on peak foraging activities. Such studies classified diurnal species as being active from dawn to dusk; nocturnal species as foraging from dusk or later to dawn; and cathemeral species as having activity periods that raged from full day-light conditions to after dusk low light conditions, or as having pronounced variation in activity across seasons (i.e. diurnal in winter, nocturnal in summer) (Schmitz and Motani 2010).

Phylogeny: I used the time-calibrated species level phylogeny of Jetz et al. (2012). A set of 100 trees was generated based on the list of species for which I had data. The trees were generated from the Ericson (2012) backbone phylogeny, which uses only genetic data to model the trees. One species for which I had trait data, *Anas wyyilliana* was dropped from the tree as there was no phylogenetic data for this species. During statistical analysis in the ‘R’ platform, one sample tree was selected for trait mapping as a first approximation (note that future analyses should repeat the analyses over a larger tree sample). Species for which specific trait data was missing were subsequently dropped from the tree during analysis.

Statistical analysis

Body mass: Body mass for both female and male birds separately was then mapped onto the phylogeny by reconstructing the history of a continuous trait (body mass) with the contMap() function in the phytools package (Revell 2012) for the statistical platform 'R' (R Core Team 2013). This method estimates the states at the internal nodes using a maximum likelihood approach and then interpolates the states along each edge. That is, based on the trait values at the tips and internal nodes, values along the branch edges are estimated and mapped as a continuous transition from trait value to trait value at each end of the branch.

Discrete traits: After being classified, the ecological traits (diving, diel activity pattern, and diet) were mapped, as ancestral state reconstructions, onto the phylogeny (Jetz et al. 2012). This was done using maximum likelihood ancestral state reconstructions with the ace() function in the ape package (Paradis et al. 2004) for the statistical platform 'R' (R Core Team 2013), assuming that evolutionary transitions between different character states have the same rate. The maximum likelihood approach to reconstructing ancestral states uses a given model of the process under investigation to predict the evolutionary transitions that would most likely lead to the observed data. That is, given some statistical model of the way evolution proceeds, the ancestral character states are reconstructed in a way that make the character states of contemporary species most probable. Assuming that a phylogenetic tree and its branches are known and fixed, while the character states at the nodes are not known, this approach seeks to derive statements that can be used to suggest if one value at a node is more or less likely than some other (Pagel 1999).

Phylogenetic ANOVA: Finally, we compared the ecological traits to body mass to test if certain character states were larger than others using a phylogenetic ANOVA. We used the phyl_anova () function in the geiger package (Harmon et al. 2008) for the statistical platform 'R' (R Core Team 2013). Unlike a normal ANOVA, a phylogenetic ANOVA takes the hierarchical nature of phylogenetic descent into account when comparing variants. This is important because species in a phylogeny may not represent independent data points, so the use of conventional parametric and nonparametric methods may not be appropriate to test hypotheses in interspecific data. A phylogenetic ANOVA accounts for this problem by incorporating phylogenetic information like topology and branch length into the analyses (Garland et al. 1993).

Results:

Ancestral State Reconstructions:

Body mass

The continuous trait maps of female and male body mass show a remarkably similar pattern of body mass evolution (Fig. 1 & 2), with trait values that indicate the generally smaller size of females. Males have a body mass range of 364-11,900 g, while females have a range of 318-10,300 g, with the lightest masses are depicted in red and the heaviest masses in blue. Most of the tips, representing the observed species data, for both male and female, are depicted in red, which has an approximate range of 300-1,000 g. The ancestral mass for all Anseriformes is depicted in orange representing an approximate mass of 1500-1900 g in females and 1600-2200 g in males. The species group of *Cygnus,* swans, stands out as heaviest (shown in blue), and the groups of *Branta* and *Chen*, geese appearing to secondarily evolve smaller masses, and *Somateria,* eiders, appear to secondarily gain slightly larger masses.

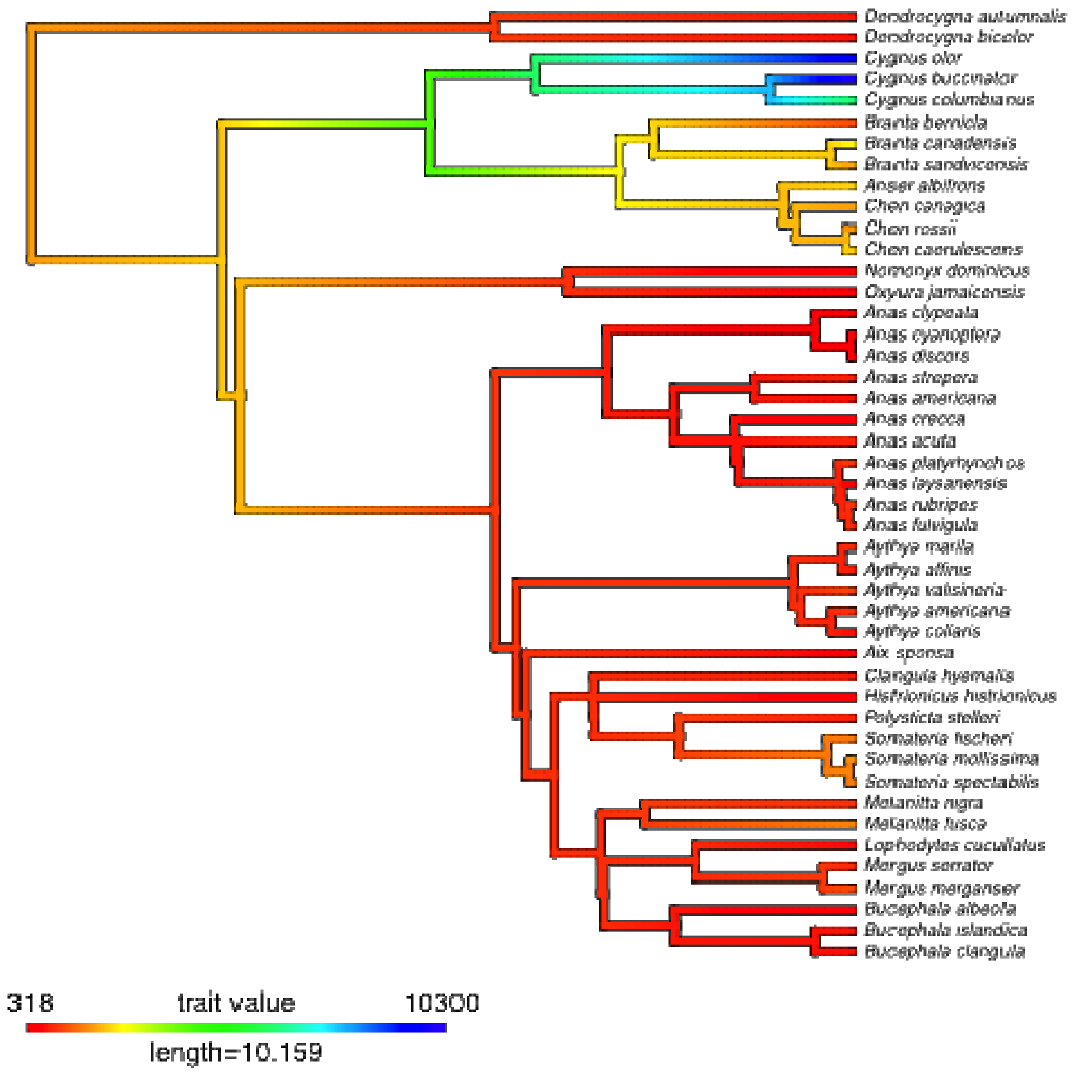

Fig. 1: Continuous trait map of female body mass.

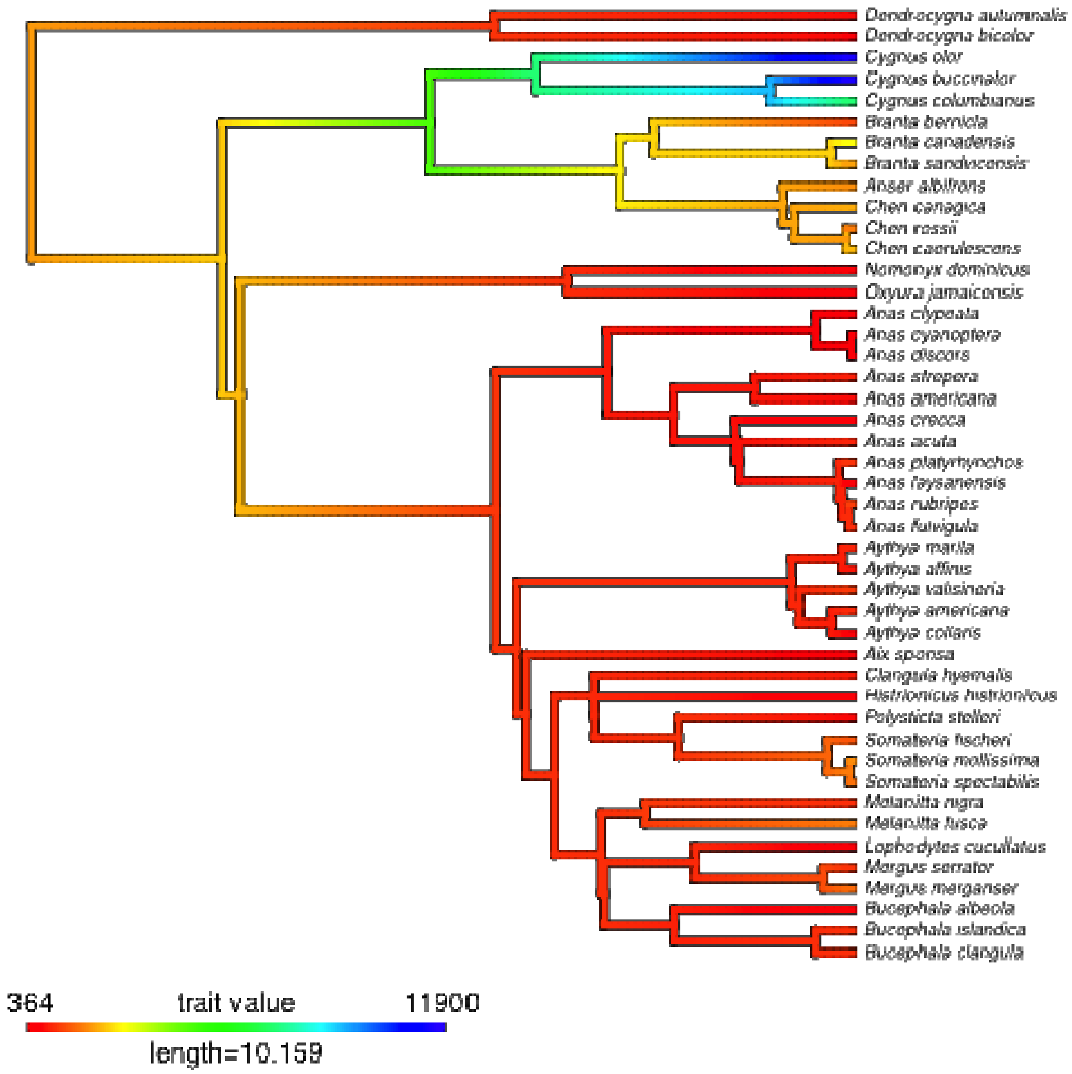

Fig. 2: Continuous trait map of male body mass.

Diving behavior

Most species examined, 39 out of 46, were diving. The appearance of non-diving species appears to independently occur five times in the phylogeny, and it appears that in these species diving is secondarily lost (Fig. 3). Diving is lost in three duck species: *Dendrocygna autimnalis*, *Anas streptera*, and *Anas laysanensis*, and in four species of geese: *Branta bernicla*, *Branta sandvicensis*, *Chen rossii*, and *Chen caerulescens*.

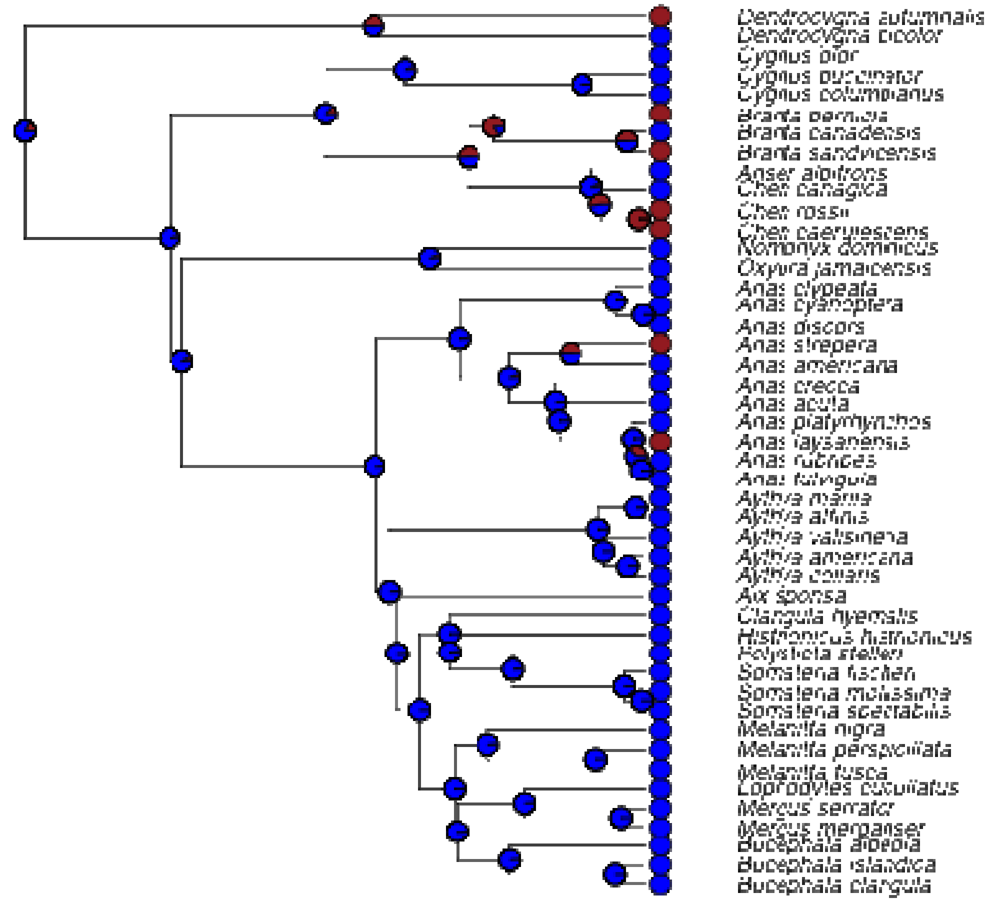

Fig. 3: Ancestral state reconstruction of diving locomotory activity (blue=diver, brown=non-diver).

Diet

The ancestral state reconstruction of diet shows that the ancestral node is most likely characterized herbivory or omnivory. Carnivores only secondarily evolved within omnivores, possibly with two independent origins, one at *Anas laysenensis* and one at the node where *Aythya* species diverge from eiders, mergansers, and scoters.

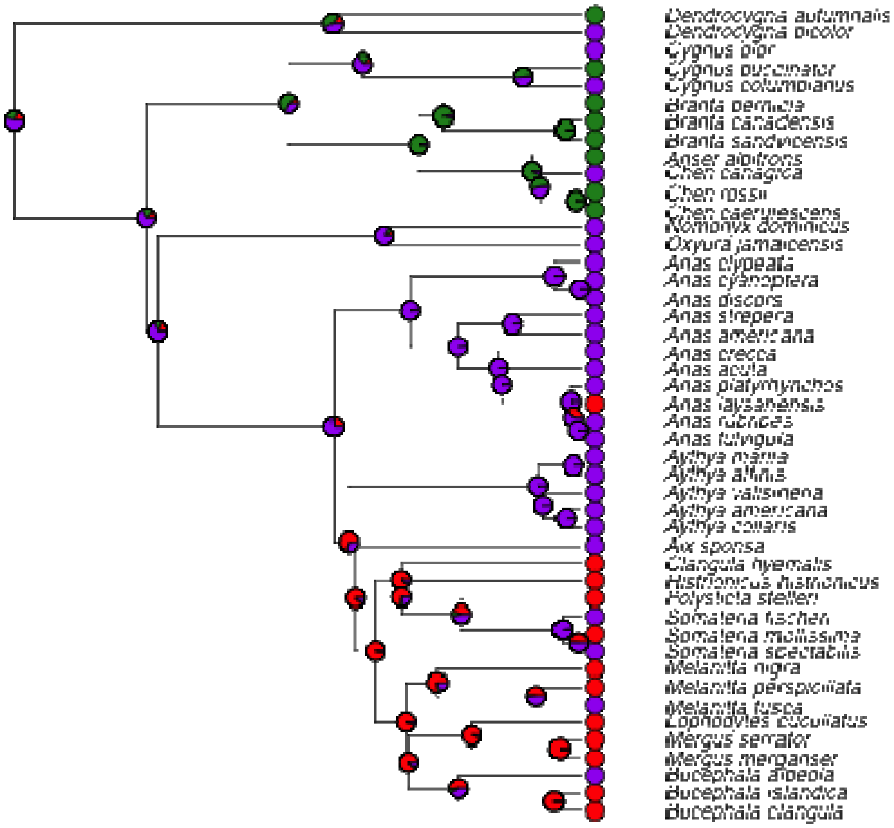

Fig. 4: Ancestral state reconstruction of diet (green=herbivorous, red=carnivorous, purple=omnivorous).

Diel activity patterns

The ancestral state reconstructions of diel activity patterns show a very low degree of resolution at the internal nodes, suggesting the highly plastic nature of this trait (Fig. 5). A reduced model comparing diurnal to non-diurnal species shows somewhat more resolution at the nodes, but with most internal nodes predicting a fifty/fifty likelihood for either state (Fig. 6).

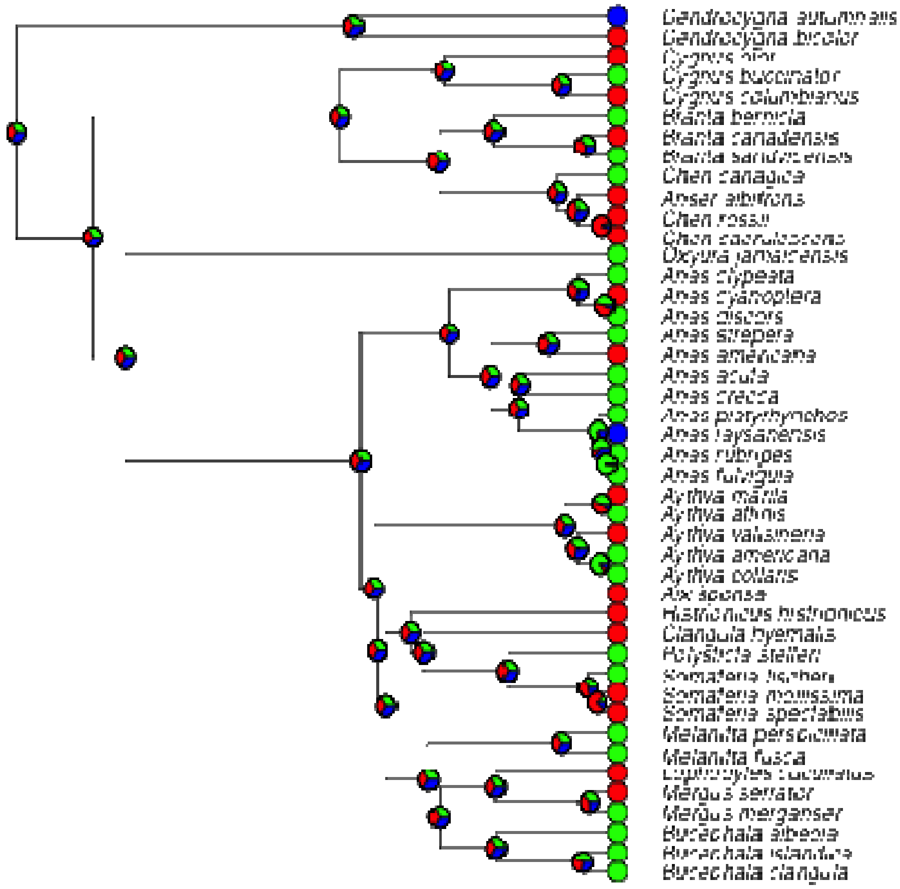

Fig. 5: Ancestral state reconstruction of diel activity patterns (blue=nocturnal, red=cathemeral, green=diurnal).

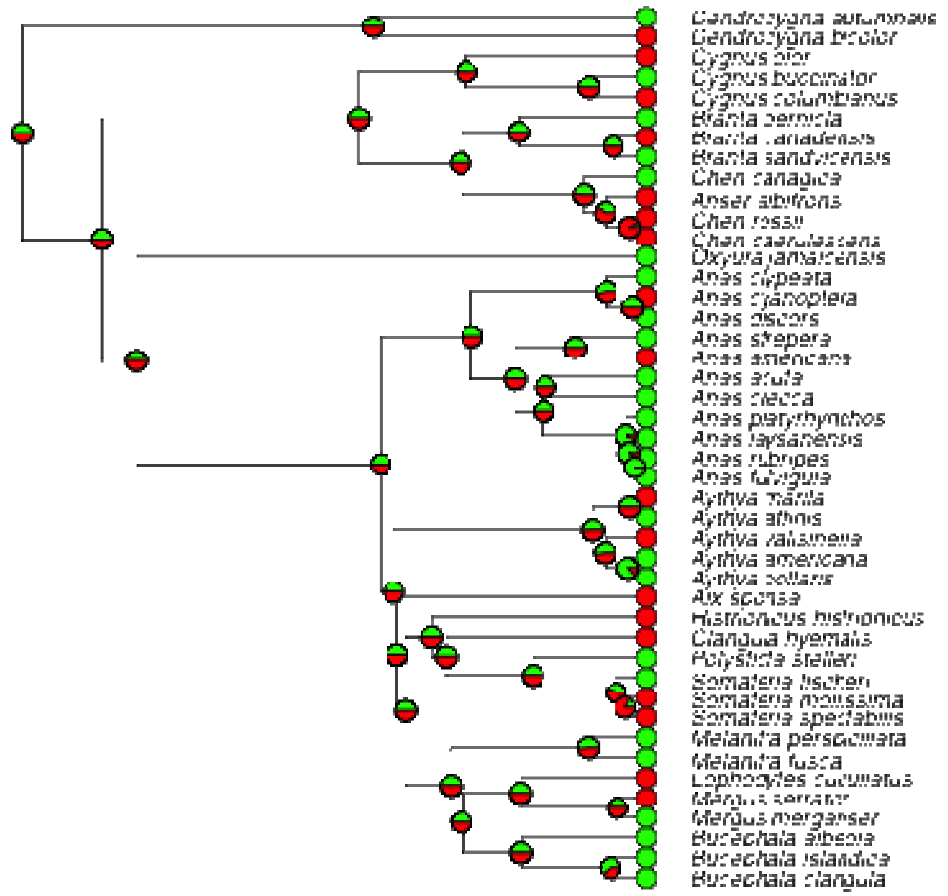

Fig. 6: Ancestral state reconstruction of activity pattern (green=diurnal, red=non-diurnal).

Phylogenetic AVOVAs and box plots:

Visually it appears that herbivorous diet may be associated with larger body size, but for both males and females there was no significant difference in body mass between the three diets (Fig. 7 & 8). There was no significant difference between divers and non-divers in terms of body mass in either males or females, however, all of the outliers (represented as open circles) were divers (Fig. 9 & 10). There was no significant difference in body mass, for males or females, related to diel activity patterns (Fig. 11 & 12).

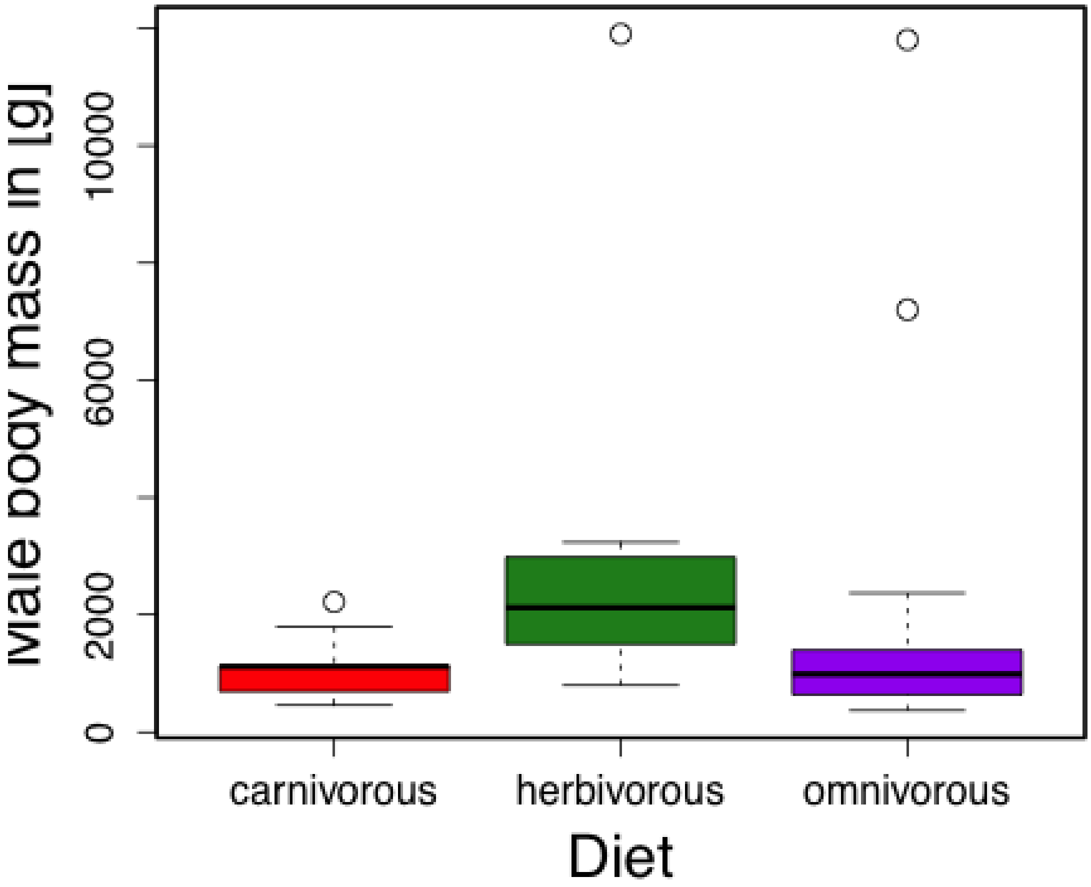

Fig. 7: Box plot for male diet. (p=0.6553).

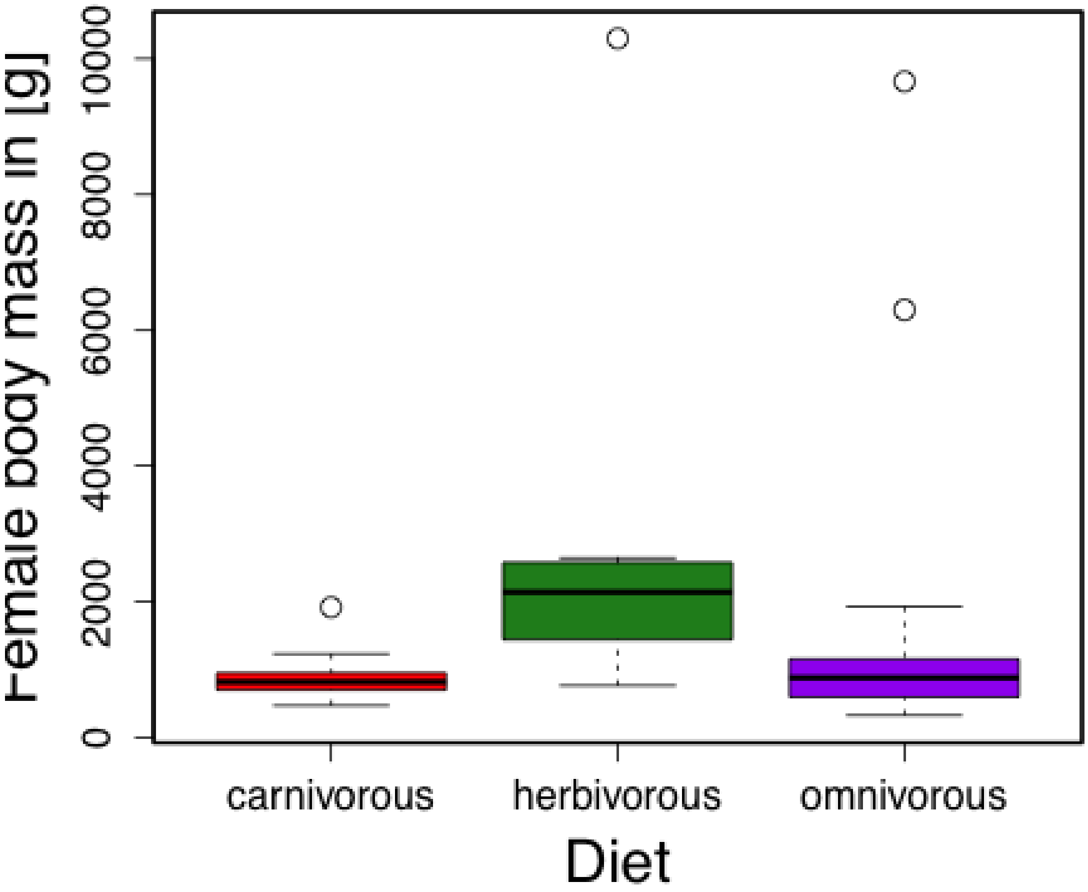

Fig. 8: Box plot for female diet (p=0.5954).

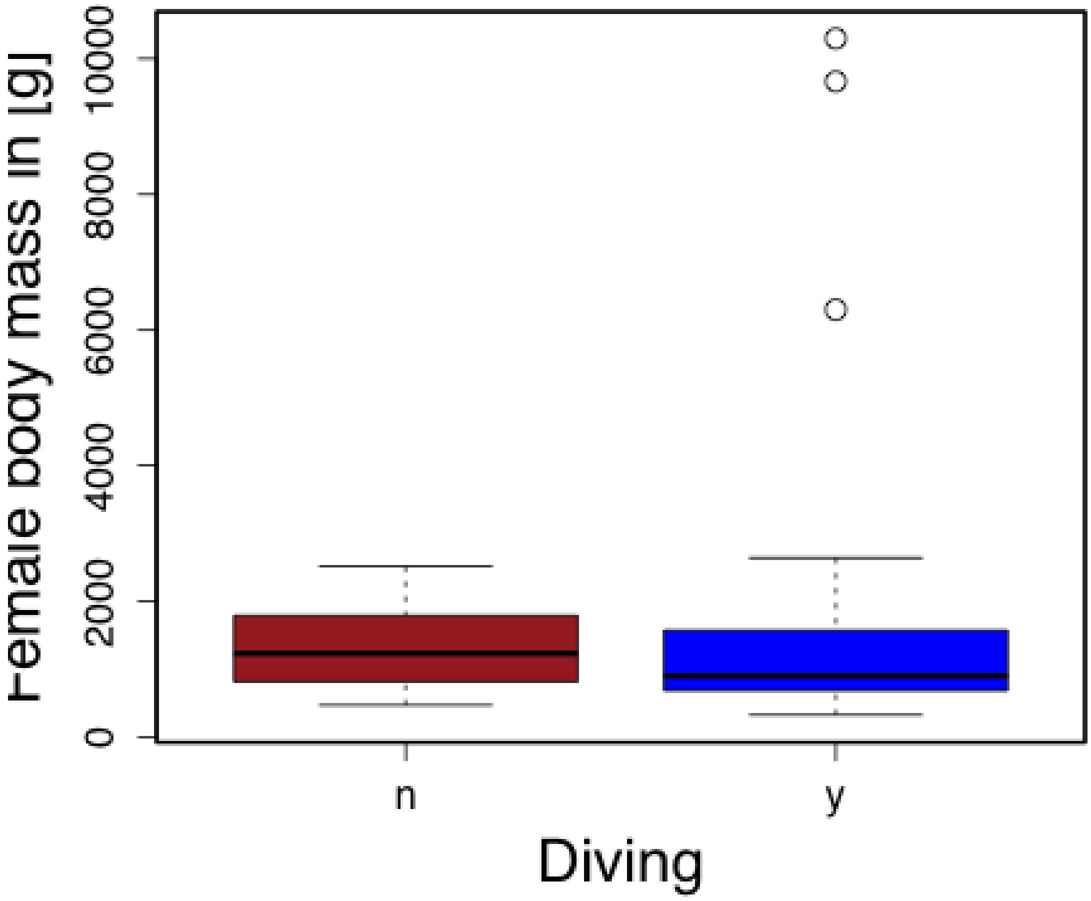

Fig. 9: Box plot for female diving (n=non-diver, y=diver) (p=0.8811).

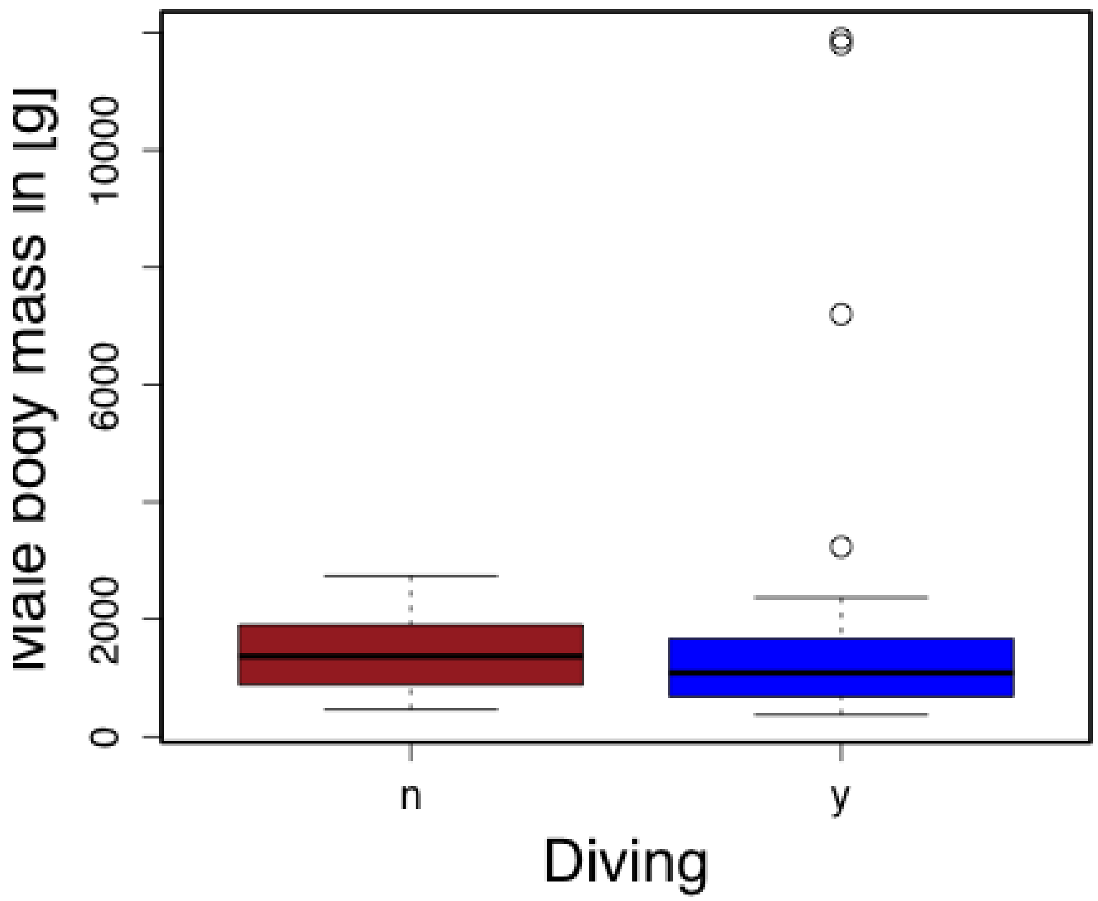

Fig 10: Box plot for male diving (n=non-diver, y=diver) (p=0.8482).

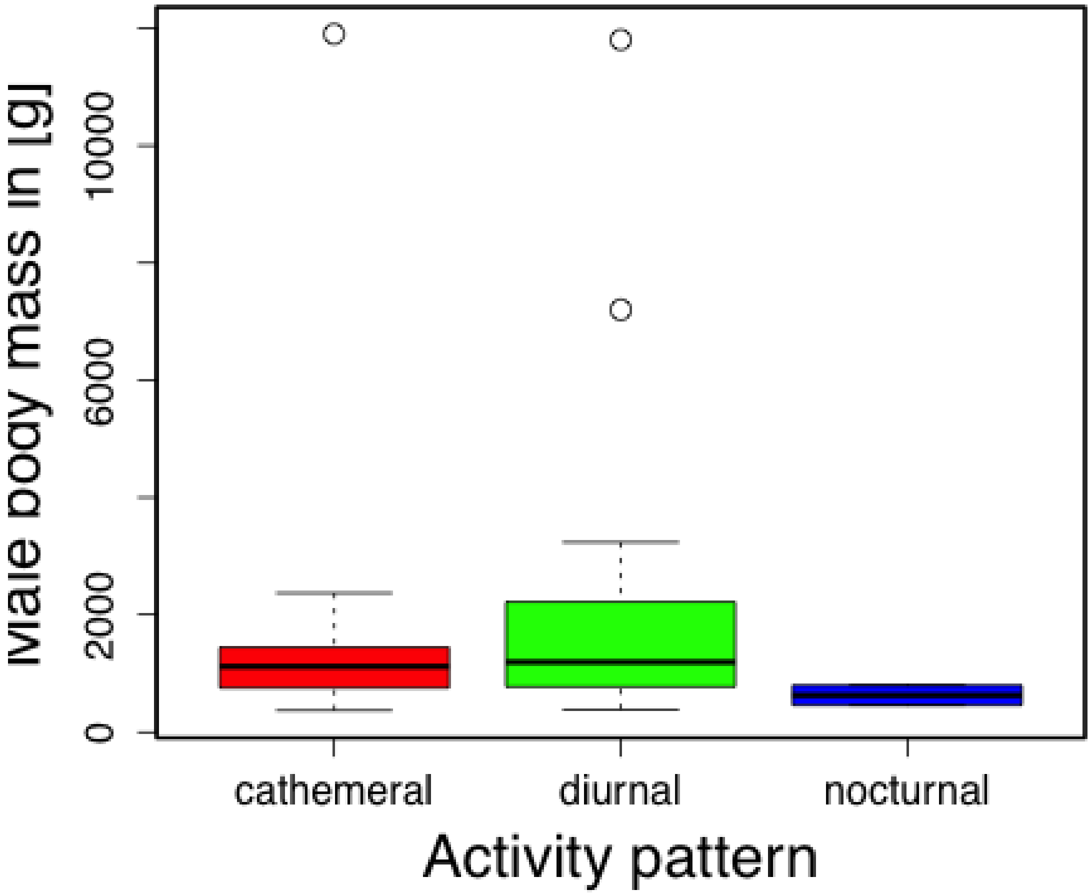

Fig. 11: Box plot for male activity pattern. (p=0.6833).

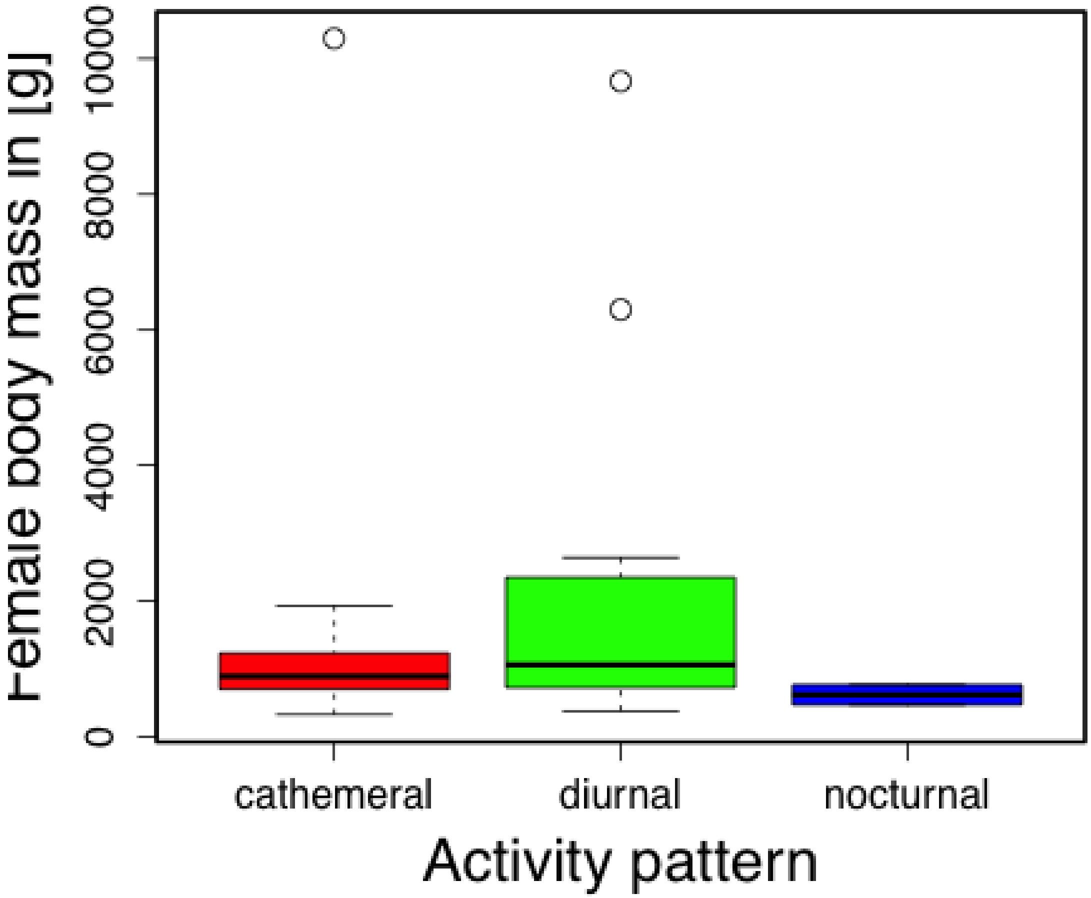

Fig 12: Box plot for female activity pattern (p=0.6553).

Discussion:

By looking at how morphological and ecological traits evolved across the phylogeny of Anseriformes, we hoped to better understand the ways in which these species adapt to fill ecological niches, and the ways in which these traits relate to and impact one another. In general, we found that body mass in males and females evolved in a remarkably similar fashion, suggesting that selective pressures influenced the body masses of both sexes of these species in similar ways. In the ancestral state reconstruction, it appears that diving locomotion is the ancestral state for Anseriformes, with non-diving independently evolving five times. A more nuanced look at why diving may have evolved or been lost, separating forage diving and escape diving could help elucidate what pressures factored into these independent transitions. For diet, the ancestral state appears to be either herbivory or omnivory, with carnivory secondarily evolved twice independently, and only within omnivores. This pattern seems consistent with studies on the diet evolution in mammals that show all transitions to specialized diets (herbivory and carnivory) involving omnivory (Price et al. 2012). The ancestral state reconstruction for diel activity pattern showed little resolution at the internal nodes, indicating that in Anseriformes this trait is highly plastic. This finding was a bit surprising, as previous studied have indicated that within a subgroup of Anseriformes, *Aythya*, there is an evolutionary graduation from diurnality to nocturnality (Livezey 1996). We also found that body mass was not significantly correlated with any particular diet, diving locomotion, or diel activity pattern. This was unexpected, as many studies have indicated the evolutionary relationship between body weight and ecology, such as the range of foods consumed and the structure of habitats (Clark 1976). However, since annual or single-season averages of masses were used, it is possible that seasonal plasticity of body mass, diel activity pattern, and diet are correlated in more nuanced ways.

From the continuous trait maps of male and female body mass (Fig. 5 & 6) we saw that male and female body mass evolved in very similar patterns, with trait values reflecting the generally smaller masses of females. However, the masses used were average values that do not account for seasonal plasticity in body mass. For example, in *Bucephala albeola* male and female body mass fluctuates throughout the year, with males peaking in mass in December, and having smallest mass in May-August, while females peak in mass during

March-May and are at their lightest at the end of incubation (see Appendix). It would, however, be interesting to find the differences between male and female body masses for study species, and map the differences onto the phylogeny in order to see where sexual dimorphism in body mass evolved. In other words, look at where in the phylogeny transitions to more similar or disparate body masses occurred between the sexes.

For locomotory behavior we found that the trait of non-diving appeared to be a secondary loss of diving behavior (Fig. 3). In the species examined there appeared to be five independent transitions to non-diving. Locomotion is also an important indicator of how species exploit their environment, as there are energetic costs associated with different locomotor strategies. Species that are anatomically well-adapted for diving and underwater swimming often sacrifice aerial agility to fulfill foraging requirements. Surface feeders, on the other hand, have legs that are placed relatively forward on the body and are close together, which improves their walking movements and increases their ease of takeoff (Johnsgard 2010). Body shape, body size, and buoyancy are all determinants of the locomotor costs of diving in birds. Body shape affects hydrodynamic drag; body size affects the kinematics and aerobic efficiency of foot paddling versus underwater "flying"; and buoyancy affects the relative costs of descent, foraging, and ascent (Lovvorn 1991). Birds associated with aquatic environments employ diverse locomotory strategies while feeding, including a) catching prey at the surface of the water while airborne; b) tipping up, dipping their head or part of the body into the water; c) penetrating through the water column using gravity; d) grazing on the aquatic surface and substrate under water; and d) actively chasing prey under water (Hinic-Frlog and Motani 2009). Each of these strategies requires moving the body in different ways, employing different body parts, thus it makes sense that birds with different feeding locomotory strategies have different morphologies. There was no significant relationship between body mass and diving found, for either males or females, however, all of the outliers, which had significantly larger body masses, were divers. This is consistent with literature that suggests larger body mass provides an advantage to diving. Large body mass is expected to enable animals to dive for longer, as oxygen storage capacity scales isometrically with body mass, while rate of oxygen metabolism scales allometrically with body mass. This potential for longer dives, also allows prolonged transit duration, which could allow for deeper dives (Halsey 2006). However, as noted before, only the outliers are consistent with this idea, and overall there was no significant difference in body mass.

For diet, it appears that the Anseriformes evolved from an herbivorous or omnivorous ancestor, and that carnivory was secondarily evolved with possibly two independent origins (Fig. 4). Across the clade, herbivory and carnivory are grouped together separately with a large group of omnivores between them, suggesting that a transition through omnivory was necessary for carnivores to evolve. Studies of mammalian diet show a similar pattern in which some clades are almost exclusively carnivorous or exclusively herbivorous, while some clades appear to switch frequently between herbivory and omnivory, or between omivory and carnivory, but not between herbivory and carnivory. The transition rate between herbivory and carnivory in mammals is approximately zero, and almost all trophic transitions in mammals involve omnivory (Price et al. 2012). Adaptations associated with foraging are important in Anseriformes, with bill shape and leg placement being important, as structural modifications can influence how waterfowl achieve a maximum degree of habitat exploitation with a minimum of interspecies competition for the same food. Bill shape is closely associated with the types of foods taken, for example the bills of swans are adapted for tearing and consumption of submerged aquatic plants, while scoters and eiders have bills suited for heavy mollusk-crushing, These changes in bill shape allow different species to exploit different parts of habitats (Johnsgard 2010). Since we see morphological differences among species with different diets, we speculated a corresponding distinction in body mass associated with differing diets. However, a phylogenetic ANOVA showed that there was no significant difference in body mass for species of the three diet types. One possible reason that there was no significant difference is that body mass and diet are highly variable throughout the year for many species. Many species may shift from herbivorous or carnivorous diets to an omnivorous diet with shifts in the breeding cycle or seasonal availability. For example, *Anas americana* eats an almost entirely herbivorous diet during the winter and migration, but shifts substantially to non-plant foods during laying and breeding seasons. At the same time body masses of *Anas americana* shift considerably throughout the year with males in the fall ranging from 676-948 g, while males in the spring range from 681-851 g, and females in the fall ranging from 640-806 g, while females in the spring range from 635-744 g (see Appendix). By looking at average body masses, and classifying variable diets as omnivore rather than seasonal herbivores or carnivores, the nuances of this plasticity may be missed.

The ancestral state reconstruction of diel activity patterns showed a very high degree of plasticity in this trait. Almost all of the internal nodes predicted that all three activity patterns (nocturnality, diurnality, and cathermal) were equally likely (Fig. 5). Since there were only two nocturnal species in the study group, and since they were not closely related, it was speculated that they were negatively influencing the likelihood estimates, so a second ancestral state reconstruction was performed with cathemeral and nocturnal species reclassified as a single, non-diurnal state. This reconstruction found somewhat higher resolution at the nodes, but still showed most nodes as being equally likely for either state (Fig. 6). These findings differed from a phylogenetic study of pochards (Aythyini), a subfamily of Anseriformes that includes the genera *Netta* and *Aythya*, which predicted an ancestral state of diurnal and saw two changes in the tribe away from diurnality. This study saw a change from diurnal to crepuscular (active during twilight hours) at the ancestor, and then a shift from crepuscular to nocturnal at the transition from *Netta* species to *Aythya* species (Livezey 1996). The Livezey study showed a resolved and directional pattern of diel activity pattern evolution that was not seen in this study of Anseriformes. However, all of the overlapping species between these studies were classified differently; all five overlapping *Aythya* species were classified as nocturnal in the Livezey study, but in this study three were classified as diurnal (*americana*, *collaris*, and *affinis*) and two were classified as cathemeral (*valisineria* and *marila*). Although we did not see any clear pattern of diel activity pattern evolution across the phylogeny we predicted that body mass may be correlated with different diel activity patterns, as previous studies have indicated that certain morphologies are related to ecology and behavior. Eye size has been related to activity pattern, the time of day when an animal is awake and active, as the patterns are associated with different levels of light. Birds adapted for photopic vision associated with diurnal patterns have eye shapes optimized for visual acuity, while birds adapted for scotopic vision associated with the low-light of nocturnal patterns have eyes that exhibit larger corneal diameters and axial lengths than photopic birds (Hall 2007). A study of terrestrial amniotes, using macro-anatomical structures as proxies for optical parameters, showed that diel activity patterns are strongly reflected in the morphometrics of the eyeballs, and that nocturnal, cathemeral/crepuscular, and diurnal species occupy distinct areas in the morphospace (Schmitz and Motani 2010). Additionally, the morphological trait of body size is important as it puts physiological limitations on birds, which can influence time budgets. According to the body-size hypothesis, body size directly affects time spent feeding or forage intake rates via energetic processes. Smaller species generally feed for greater portions of the day (≥80%) to maintain their basal metabolic rate (BMR) during periods of declining ambient temperatures, and may be relatively less able to adjust their feeding budgets in response to declining temperatures compared to larger species, as larger birds have relatively larger reserves and can devote smaller portions of their daily energy intake to maintain their BMR (Jonsson 2009). When comparing activity pattern to body mass in a phylogenetic ANOVA, no significant difference was found among the three activity patterns (Fig. 11 & 12). Like diet, the nuances of activity patterns were lost in classifying species into discrete traits. It was noted in certain species, such as *Cygnus buccinators*, that the percentage of time spent foraging during the day or at night varied with season, age, sex, reproductive conditions, weather, and habitat. For other species, such as *Branta bernicla* and *Chen canagica,* foraging was apparently less linked to time of day, but rather to tidal cycles, with feeding patterns relating to high or low tide. Further, some species appeared to be primarily diurnal foragers, but would forage at night during the full moon, like *Anas clypeata* and *Cygnus columbianus* (see Appendix). It was also noted that some typically diurnal species were pushed into nocturnal feeding due to human interventions such as hunting, *Chen rossii* and *Anas americana* for example (see Appendix).

To conclude, while no obvious patterns of coevolution emerged in the traits studied, the analyses yielded several interesting findings that upon further study could provide information on how morphological evolution and ecological transitions relate to one another in Anseriformes. It appears that most non-divers also happen to be herbivores (5/7 non-divers were herbivores) suggesting a possible correlation between these traits within the clade. However, with such a low sample size of non-divers, greater investigation would be required to see how well this hypothesis holds up. It also appears that these traits did not co-vary together, as the closest common ancestor of the four closest related species (*Chen* and *Branta* species) is most likely an herbivorous diver (Fig. 3 & 4). While there was no significant correlation found between body mass and diving locomotion, there was an indication that especially large (greater than ~6000 g) species were divers (Fig. 9 & 10). However, since these species were outliers in the phylogenetic ANOVA, and since there were only three species of this size, *Cygnus columbianus, Cygnus_olor,* and *Cygnus_buccinator,* it would be interesting to study a wider sample of species of this size to see if this apparent pattern holds up. As discussed earlier, studies suggest larger body mass provides an advantage to diving (Halsey 2006), however, it is possible that there is a threshold mass where foraging becomes the most advantageous feeding strategy. Finally, among the species studied only two were clearly nocturnal, *Dendrocygna autumnalis* and *Anas laysanensis*, and there was very little resolution at the internal nodes of the ancestral state reconstruction for diel activity pattern (Fig. 5). It would be interesting to sample a group that included more nocturnal species to see if any pattern more clearly emerges, and if this pattern shows any relationship to the evolution of body size, diving locomotion, or diet.

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