5-2014

Olfactory Ratio as a Potential Proxy for Behavior in Theropoda

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Olfactory Ratio as a Potential Proxy for Behavior in Theropoda

A thesis submitted in partial fulfillment of the requirement
for the degree of Bachelor of Science in Geology from
The College of William and Mary

by

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April 30, 2014

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Abstract

      Olfactory ratio is frequently used as a proxy for olfactory acuity in extant Aves, and because it can be reconstructed from the fossil record, it is applicable to non-avian theropods as well. Extant avian taxa show a remarkable diversity in olfactory lobe size and morphology; however, the significance of this diversity is unclear. Previous authors have correlated olfactory ratio with various ecological traits; however, all of these, except for event timing, have been shown to be non-significant once body size is accounted for. In this study, mating system, event timing, pair bond length, migratory behavior, parental care, and diet were all investigated as potential predictor variables of olfactory ratio in extant birds. Results showed that contrary to the results of previous analyses, event timing was not a significant predictor of olfactory ratio when phylogenetic non-independence was adequately controlled for. A weak correlation between diet and olfactory ratio was demonstrated, with insectivorous birds possessing relatively higher olfactory ratios. However existing paleontological data suggests that those species which may have been insectivorous likely did not possess high olfactory ratios.

Introduction:

The ecological significance of the wide disparity in olfactory bulb size in extant Aves has remained largely unclear, despite several decades of work (e.g., Bang, 1971; Healey and Guilford, 1990). In this study, 122 extant avian species were investigated in an attempt to better understand the underlying ecological explanations for this remarkable diversity. To this end, pair bond length, mating system, event timing, migratory habits, parental care, and diet of species were investigated for potential correlations with olfactory ratio.

A growing body of work on the use of olfactory cues in the mating behavior of extant Aves exists (e.g., Bonadonna and Nevitt, 2004; Mardon et al., 2011). In several species, olfactory cues have been shown to be instrumental in sex, mate, and nest recognition (e.g., Bonadonna et al., 2003; Mardon et al., 2010, 2011). The ability to efficiently distinguish one's mate and nest are presumably important in strongly monogamous species. *Thus, I hypothesize that those species that are monogamous and maintain long-term pair bonds will, on average, have a higher olfactory acuity, and consequently higher olfactory ratios.*

In addition to mating behavior, a number of other ecological variables were examined in this study for possible correlations to olfactory ratio, based upon a substantial body of research connecting each to various olfactory cues. *It is hypothesized that nocturnal, migratory, altricial, carnivorous, and scavenging species will have higher olfactory ratios compared to other taxa.*

Extant Aves are considered to be the closest modern analogues to non-avian theropods and, as such, represent a study system through which researchers can learn about behavior in the latter (e.g., Ostrom, 1976; Erickson et al., 2009; Zelenitsky et al.,

2009). Olfactory ratios can be extracted from the fossil record with relative ease and, as in extant Aves, are considered to represent an accurate proxy for olfactory acuity in this taxon (e.g., Zelenitsky et al., 2009). This property, combined with the presumed connection between olfactory ratio and one or more ecological variables suggests that olfactory ratio could also be a useful proxy for behavior in non-avian theropods. Indeed any strong correlations between olfactory ratio and behavior in extant Aves may have also existed in extinct theropods.

Olfactory Ratio

Much of the comparative work on avian olfaction has focused on the morphology and relative size of the olfactory bulbs of the brain (e.g., Bang and Cobb, 1968; Bang, 1971; Healey and Guilford, 1990). These bulbs project ventrally and anteriorly from the forebrain of vertebrates and are critical to the process of olfactory signaling (Vassar et al., 1994; Purves et al., 2001; Zelenitsky et al., 2011). The binding of odor molecules to olfactory receptor neurons embedded within the olfactory epithelium results in the propagation of a signal, which is passed to the olfactory bulbs via axons which eventually coalesce to form the olfactory nerve (Vassar et al., 1994; Purves et al., 2001). The olfactory lobes collect and process this information and transmit it to higher neural centers via the olfactory tract (Mori et al., 1999; Purves et al., 2001). Thus, the olfactory bulbs are important relay stations along the path from olfactory stimuli to behavioral response. The relative size of the olfactory bulbs is commonly expressed as an olfactory ratio, which is defined as the largest linear dimension of the olfactory bulb, standardized

to the largest linear dimension of its corresponding cerebral hemisphere (Fig 1; Cobb 1960; Bang and Cobb, 1968; Zelenitsky et al., 2009; Zelenitsky et al., 2011). This method was first employed by Cobb (1960) and olfactory ratio has been used extensively as a proxy for olfactory acuity in avian taxa since (e.g., Bang and Cobb, 1968; Bang, 1971; Ioalé and Papi, 1988; Zelenitsky et al., 2011).
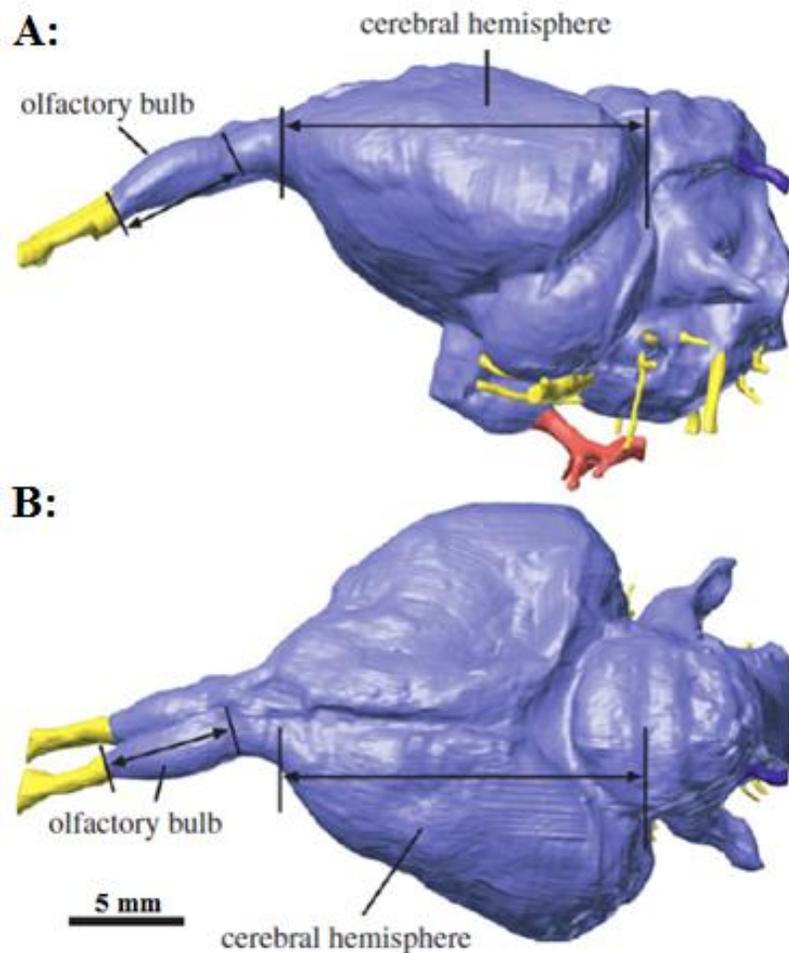
Figure 1: Lateral (**A**) and dorsal (**B**) view of a virtual brain endocast from the extinct avian species *Lithornis plebius*. The largest linear dimension of the left olfactory bulb and its corresponding cerebral hemisphere are indicated (modified from Zelenitsky et al., 2011).

The hypothesized link between the relative size of the olfactory bulbs and the olfactory acuity of a species stems from the assumption that the size of sections of the

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brain are positively correlated with the importance of their associated function (Bang and Cobb, 1968; Healey and Guilford, 1990; Zelenitsky et al., 2011). This relationship is known as the principle of proper mass (Zelenitsky et al., 2011) and several studies have presented evidence supporting its validity in avian taxa (e.g., Nottebohm et al., 1981; Krebs et al., 1989). Some author have also explored the physiological basis for the predicted correlation between olfactory ratio and olfactory acuity. Wenzel and Meisami (1987) demonstrated a positive correlation between olfactory bulb size and the number and size of mitral cells (major neural outputs of the olfactory bulbs, Purves et al., 2001), suggesting that those taxa with larger olfactory bulbs relay more olfactory information to higher centers of the brain. In an investigation of olfactory receptor genes in nine avian species, Steiger et al. (2008) showed a positive relationship between olfactory ratio and the total number of genes coding for olfactory receptors. These findings suggest that species with higher olfactory ratios may express a wider variety of olfactory receptors and thus be able to detect a wider array of odorants (Niimura and Nei, 2006; Steiger et al., 2008).

The use of olfactory ratio as a potential proxy for olfactory acuity in non-avian theropod taxa is dependent on its reliable preservation in the fossil record. The olfactory bulbs of theropod species were confined by two bones of the skull, sthe frontals and lacrymals (Brochu, 2000). Impressions left by olfactory bulbs are visible on the former (Brochu, 2000; Zelenitsky et al., 2009). Additionally, the ethmoid process, an ossified structure which is present in many non-avian theropod species, can be used to reconstruct the olfactory bulbs of fossilized specimens (Ali et al., 2008). This structure has been shown to be homologous to structures associated with the olfactory bulbs of extant

archosaurs (including Aves), suggesting that its use in olfactory reconstruction is justified (Ali et al., 2008). The olfactory bulbs of non-avian theropods can be visualized via the construction of brain endocasts, which is commonly accomplished by means of CT scanning (Fig 2; Brochu, 2000; Zelenitsky et al., 2009). In these endocasts, the olfactory bulbs are visible as bulges just anterior to the olfactory canal and their largest linear dimension, along with those of the cerebral hemisphere, can be calculated (Zelenitsky et al., 2009, 2011).
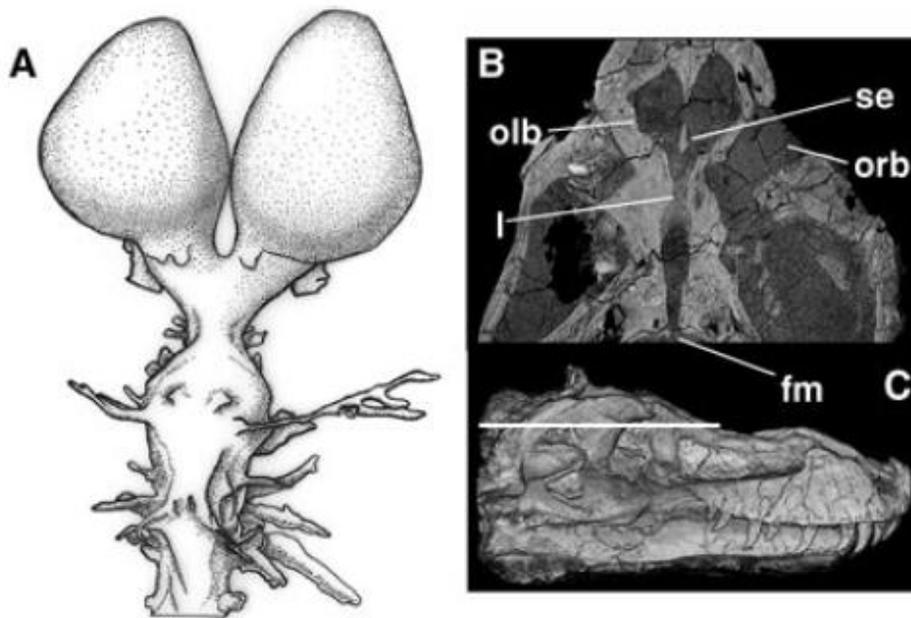
Figure 2: A: Illustration showing the dorsal view of a brain endocast produced via CT scanning of a *Tyrannosaurus rex* skull. The enlarged olfactory bulbs present in this species are clearly visible. **B:** Transverse section of the scanned T. *rex* skull, showing the location of the olfactory bulbs (olb), olfactory tract (I), a portion of the ethmoid process (se), the right orbit (orb), and the foramen magnum (fm). **C:** Right lateral view of the skull, showing the location of the transverse section shown in B (Brochu, 2000).

Zelenitsky et al. (2011) calculated the olfactory ratios of two extant avian species using endocasts and showed that the resulting olfactory ratios differed by less than 1% from fthose calculated from soft tissue measurements. As in extant Aves, the brains of

maniraptoriform theropods (e.g., Dromaeosauridae and Troodontidae) likely filled the endocranial cavity (Currie, 1995; Zelenitsky et al., 2009, 2011), allowing for accurate estimates of olfactory bulb dimensions from endocasts (Zelenitsky et al., 2009, 2011). The brains of other theropods likely did not fill the endocranial cavity, but it is assumed that the ratio between endocranial components is negligibly different from the ratios between the actual brain components (Larsson et al., 2000; Zelenitsky et al. 2009, 2011). This suggests that olfactory ratios can be calculated from well preserved specimens, with reasonable accuracy, in both maniraptoriform and non-maniraptoriform theropods.

Aves as Modern Analogue for Non-avian Theropods

The hypothesis that Aves evolved from coelurosaurian theropods during the Mesozoic Era is now widely accepted and is supported by a wealth of evidence (Ostrom, 1976; Padian and Chiappe, 1998; Erickson et al., 2009; Hu et al., 2009). The earliest known avian species, *Archaeopteryx lithographica*, dates from the Jurassic and shares a remarkable morphologic similarity to coelurosaurian theropods (Ostrom, 1976; Padian and Chiappe, 1998; Erickson et al., 2009). For example, the forelimb (Fig 3), hind limb, jaw, and skull of *Archaeopteryx* all bear a striking morphological resemblance to the corresponding structures in coelurosaurian taxa (Ostrom, 1976). In addition, many traits that were considered avian synapomorphies, such as the possession of pennaceous feathers, have also been observed in non-avian theropods (e.g., Qiang et al., 1998). In fact, recently described specimens demonstrate that pennaceous feathers were present in non-avian theropod species that predated *Archaeopteryx* (Hu et al., 2009). These findings

provide evidence to counter the stratigraphic disjunction objection that is widely cited by

authors supporting an origin of Aves outside of Theropoda (Padian and Chiappe, 1998;

Hu et al., 2009). Examinations of bone histology in basal avian species also reveal that

growth patterns were similar to those of non-avian theropods, suggesting that basal birds

were physiologically similar to the non-avian dinosaurs from which they evolved

(Erickson et al., 2009). Furthermore, the growth rates of non-avian theropods and basal

birds have exceeded those of extant ectothermic taxa, with the former groups displaying

growth rates similar to extant mammals and even some extant avian taxa (Erickson et al.,

2001, 2009).This evidence, taken together, suggests that extant avian taxa, rather than

ectothermic archosaurs, are the best modern analogue for non-avian theropods.
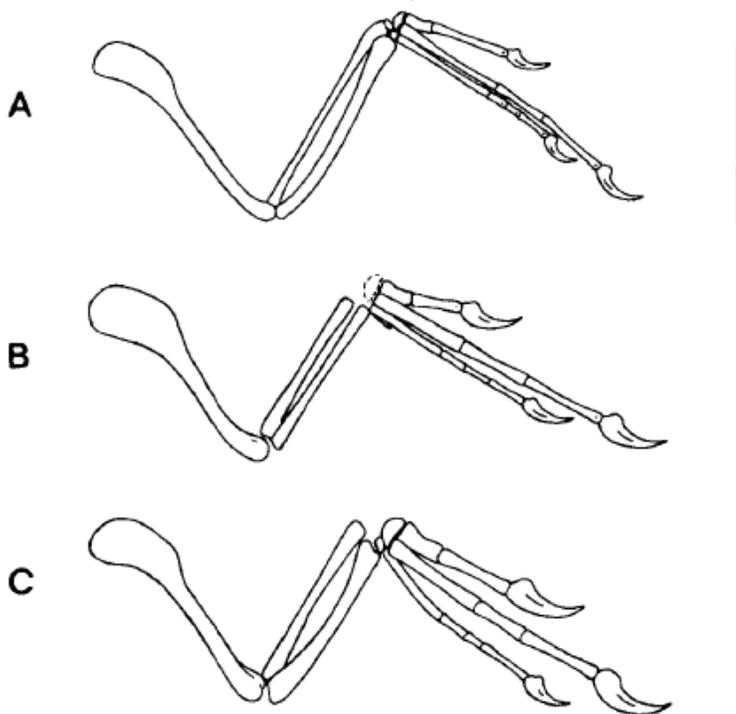
Figure 3: Diagram displaying the morphological similarity among the forelimbs of *Archaeopteryx* (**A**) and the two coelurosaurian theropods *Ornitholestes* (**B**) and *Deinonychus* (**C**). Scale bars at the right represent 5 cm (Ostrom, 1976).

Ecological Variables:

The morphology and size of the olfactory bulbs varies significantly among extant avian species (Fig 4; Bang and Cobb, 1968; Bang, 1971). Olfactory bulbs vary from the large, well developed bulbs of procellariiform species, down to the small fused bulbs of some passerine species (Bang and Cobb, 1968; Bang, 1971). This variation in olfactory bulb morphology encompasses more than an order of magnitude of variation in olfactory ratios (Bang and Cobb, 1968). The evolutionary explanation for this remarkable variation in olfactory bulb size and morphology has remained poorly understood (Healey and Guilford, 1990). Various authors have shown correlation between olfactory ratio and numerous ecological variables, including event timing (whether species shown predominantly diurnal, crepuscular, or nocturnal behavior, Healey and Guilford, 1990), diet, and breeding behavior (Bang, 1971; Healey and Guilford, 1990). Here, several new ecological variables are investigated along with several of those used in previous comparative studies.
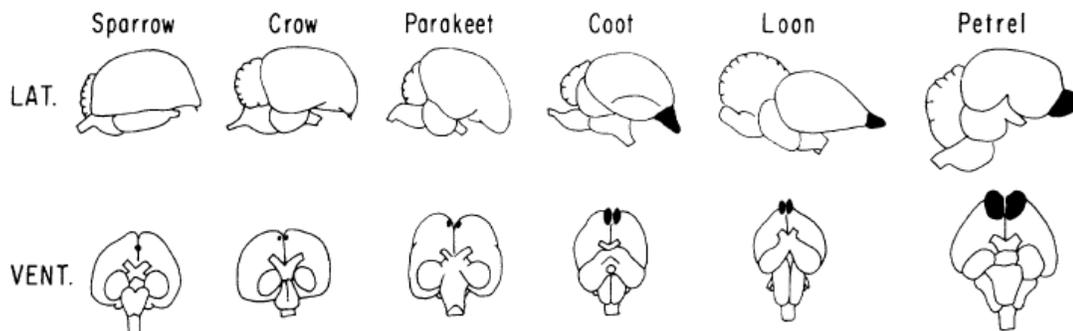
Figure 4: Diagrammatic representation of the olfactory bulb (shaded) morphology of six avian families, in right lateral and ventral views. The large disparity in size and shape of olfactory bulbs can clearly be seen (modified from Bang and Cobb, 1968).

Mating Behavior- A growing body of evidence links olfactory cues to mating behavior in several avian taxa. Much of this work has focused on the Procellariiformes, which have characteristically large olfactory bulbs and maintain long-term pair bonds (Bang and Cobb, 1968; Bonadonna and Nevitt, 2004). Studies have shown that many procellariiform species can differentiate individuals based upon scent cues, and that many show a pronounced preference for the scent of their mate above others (Bonadonna et al., 2003; Bonadonna and Nevitt, 2004; Jouventin et al., 2007). In addition, evidence suggests that procellariiform species may use the olfactory cues of their mates to aid in navigating to their nests (Bonadonna et al., 2003; Jouventin et al., 2007). Many authors have investigated the secretions of the uropygial gland as a potential source for these olfactory cues (e.g., Mardon et al., 2010). The uropygial gland, located near the base of the tail, produces waxy secretions, which are spread over the feathers during preening (Balthazart and Taziaux, 2009; Mardon et al., 2010, 2011). These secretions contain many volatile compounds and are generally considered a primary source of exogenous chemicals, which could potentially be used as olfactory cues (Balthazart and Taziaux, 2009; Mardon et al., 2010, 2011). Using gas chromatography, Mardon et al. (2010) examined the uropygial secretions of Antarctic prions (*Pachyptila desolata*) and blue petrels (*Halobaena caerulea*) and discovered that secretions had pronounced individual and species specific identities. The authors also found that secretions became sexually distinct during the breeding season (Mardon et al., 2010). Further work has also suggested that these chemical differences are preserved on the feathers of individuals after preening has taken place, thus presenting a substrate for potential chemical signals (Mardon et al., 2011). Strong individual differentiation of uropygial secretions in

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Procellariiformes could potentially facilitate *Mhc*-mediated mate selection, which

responds to olfactory cues in mammalian taxa (Zelano and Edwards, 2002; Mardon et al.,

2010, 2011). Information about the major histocompatibility complex (*Mhc*), a set of

genes which are critical to the immune responses of birds and other taxa, could

potentially inform bird of the fitness of potential mates (Zelano and Edwards, 2002).

However, more work on this potential genetic basis for mate selection is needed, in avian

taxa, to assess this hypothesis (Zelano and Edwards, 2002).

The uropygial secretions of mallard ducks have also been shown to become

sexually distinct during the breeding season, when the preen secretions of females

become distinct from those of their male conspecifics (Balthazart and Taziaux, 2009). In

addition, male mallards show dramatic changes in their sexual behavior when rendered

anosmic, via the cutting of the olfactory nerves, a response which supports the

hypothesized importance of olfactory cues in the sexual behavior of this taxon (Hagelin

and Jones, 2007; Balthazart and Taziaux, 2009). Another species which shows some

evidence for the use of olfactory cues in mating behavior is the crested auklet (Hagelin et

al., 2003; Hagelin and Jones, 2007; Balthazart and Taziaux, 2009). Crested auklets

produce a unique tangerine or citrus like odor during the mating season that is associated

with the prominent ruff-sniff display, in which individuals place their bills on the highly

scented feathers of their partner's neck during courtship (Fig 5; Hagelin et al., 2003;

Hagelin and Jones, 2007; Balthazart and Taziaux, 2009). T-maze experiments show that

crested auklets orient towards these citrus-like secretions and prefer them to foreign odors

such as banana odor (Hagelin et al., 2003). Though some evidence for alternative

hypotheses exist, it is likely that these scents play a significant role in crested auklet mating behavior (Hagelin and Jones, 2007; Balthazart and Taziaux, 2009).

Recent research shows that individual and mate recognition in some avian taxa is at least partially controlled by olfactory cues. One could easily imagine selection for greater olfactory acuity in those species that have a greater need for mate recognition (e.g., those which maintain long-term pair bonds).To test this hypothesis, pair bond length and mating system were included as variables in this comparative analysis. To date, no previous work has investigated the possible correlations between either of these ecological variables and olfactory ratio.

Figure 5: The ruff-sniff display in a crested auklet pair during courtship. During the breeding season, the feathers of the nape of the neck are highly scented and may play a significant role in chemical signaling (Hagelin et al., 2003).

Other Ecological Variables- Previous comparative analyses have investigated the potential correlation between olfactory ratio and a wide variety of ecological variables. The results of these studies have been mixed and many fail to account for potential confounding variables such as body size (e.g., Bang, 1971). However, in an effort to control for some of these variables, several have been included in this study; along with pair bond length and mating system.

In a study investigating the correlation between olfactory bulb size and six ecological variables, Healey and Guilford (1990) found a significant correlation between olfactory bulb size and event timing, which remained significant even after attempts to control for phylogeny and body size. To date, this study remains the most robust of any comparative study investigating olfactory acuity in Aves. Indeed, recent authors have even used the results of Healey and Guilford (1990) to propose adaptive explanations for olfactory bulb size in extinct non-avian theropods (e.g., Zelenitsky et al., 2009). Healey and Guilford (1990) proposed that the larger olfactory bulbs of nocturnal and crepuscular taxa could potentially be explained by an increased emphasis on olfaction to compensate for reduced visibility under low light conditions. An increased emphasis on olfactory capabilities, or other non-visual senses, in nocturnal taxa has long been observed (e.g., Crawford, 1934) and Healey and Guilford's (1990) hypothesis is consistent with these observations. Event timing has been included in the present study as a potential confounding variable and to see if the significance of the correlation to olfactory ratio holds true using the newer technique of Phylogenetic Generalized Least Squares (discussed below).

A great deal of research has been conducted on the use of olfactory cues in migration and navigation, with much of it focusing on the homing pigeon (e.g., Papi et al., 1972; Hartwick et al., 1977). For example, Hartwick et al. (1977) showed that homing pigeons which were rendered anosmic (via the insertion of tubes into their nares) performed significantly worse in homing from an unfamiliar site compared to controls and marginally worse than controls when homing from a familiar one. One hypothesized mechanism for this impaired homing is that olfactory cues are used to create an odor map

in homing pigeons, which aids in orientation and navigation to the home loft (Waldvogel, 1987). This hypothesis, if true, would provide a mechanism by which long distance migration could be accomplished, almost exclusively, via olfactory cues (Waldvogel, 1987). However, support for this mechanism is mixed and appears to be dependent on location (Waldvogel, 1987; Wiltschko, 1996). Evidence for olfactory navigation also exists in Procellariiformes. For example, Grubb (1979) observed that Leach's storm petrels preferentially approached breeding colonies from a leeward direction under low light conditions. This observation is consistent with the hypothesis that Leach's storm petrel employs olfactory cues in its terminal approach to breeding colonies. Evidence for a more complex use of olfactory cues in procellariiform navigation has also been presented. Nevitt et al. (1995) showed that several procellariiform species respond to the phytoplanktonic aerosol dimethyl sulfide (DMS) as a potential indicator of prey patches. Because DMS concentrations are correlated with ocean bathymetry (e.g., increased concentrations associated with sea mounts), they represent a potential orientational cue that could be used to aid navigation to foraging sites, or elsewhere (Nevitt et al., 1995; Nevitt, 2000). Healey and Guilford (1990) included migratory behavior in their comparative analysis and showed that no significant correlation between it and olfactory bulb size existed under the conditions of their model. Despite these findings and due to the large body of research connecting navigation to olfactory cues, migratory behavior was included as a variable in this study.

Evidence for the use of olfactory cues in parental care has been shown in several avian taxa. Cohen (1981) examined the possible role of olfactory cues in the parental care of ring doves via altering the distinct odorous excretions of newly born chicks. Ring dove

chicks are born fully altricial, and rely on the crop milk of the parents for food (Cohen, 1981). Mortality rates in chicks with altered odors were significantly higher than controls (Fig. 6) and those chicks that died weighed less than control chicks, implying a reduction in parental feeding (Cohen, 1981). These results suggest that olfactory cues could be critical in parent-offspring recognition and parental care in this species, though further research is needed to conclusively demonstrate this (Cohen, 1981; Balthazart and
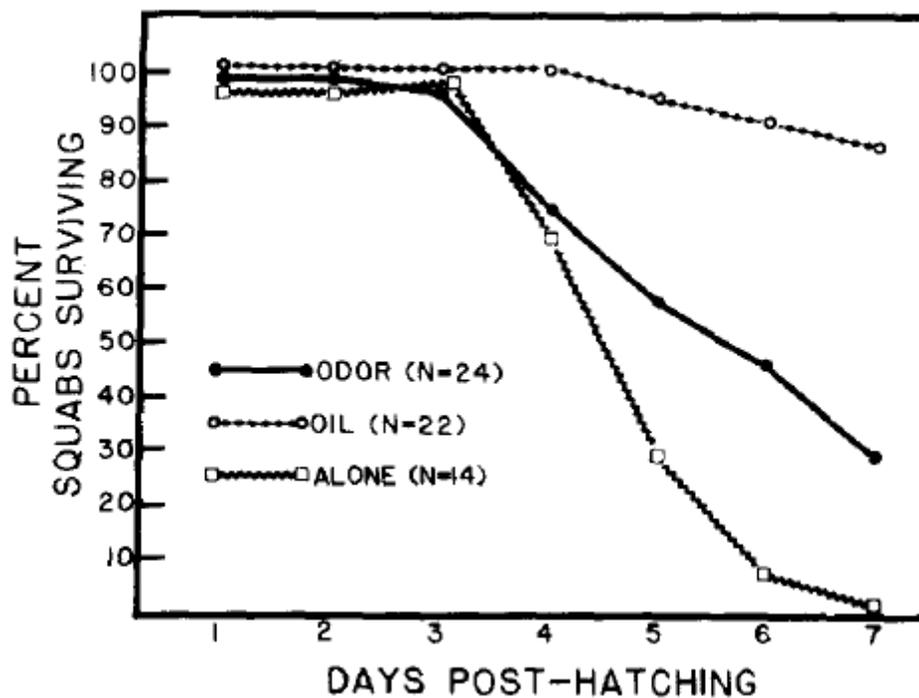
Figure 6: Graph showing the percent of chicks surviving to 7 days after hatching, in control (**oil**), odor modified (**odor**), and abandoned (**alone**) chicks. The large difference in mortality rate between odor modified and control chicks is clearly visible (Cohen, 1981).

Taziaux, 2009). An experiment on zebra and Bengalese finches, conducted by Krause and Caspers (2012), showed that during the nestling period of their young, females of both species preferred the odor of their own nest to controls. Females also avoided the nests of conspecifics when compared to a control, but showed no preference when

presented with nest odor from both species (Krause and Caspers, 2012). Despite these mixed results, it seems likely that olfactory cues play at least some part in nest recognition in these species (Krause and Caspers, 2012). Several experiments in Procellariiformes have also demonstrated the use of olfactory cues in nest localization (e.g., Bonadonna et al., 2003; Bonadonna and Nevitt, 2004). Parental behavior has been included as a predictor variable in this study, as a result of the substantial body of work connecting it to olfactory cues.

The use of olfactory cues in avian foraging is well established (e.g., Wenzel, 1971 Hutchinson and Wenzel, 1980; Nevitt, 2000). In addition, early authors hypothesized a correlation between carnivory/piscivory and higher olfactory ratios (e.g., Bang, 1971). Procellariiformes, for example, have been shown to orient towards food-related odors such as cod liver oil in the absence of visual cues, but fail to orient in response to cues unrelated to food (Hutchinson and Wenzel, 1980). In experiments on kiwis, individuals had a 100% success rate in finding food sources based upon olfactory cues alone (Wenzel, 1971). Authors have even suggested that the large olfactory bulbs of the enigmatic theropod *Tyrannosaurus rex* may have been an adaptation for finding carrion (Horner and Dobb, 1997 in Zelenitsky et al., 2009). Owing to this large body of work, diet has been included as an ecological variable in this study.

Materials and Methods

In this study, data were collected for both extant Aves and extinct non-avian theropods. The olfactory ratio, mean mass, pair bond length, event timing, migratory behavior, parental care, and diet of extant avian species was collected, while the olfactory

ratio and mean mass of non-avian theropod species were also compiled. All data used in this study were collected from a literature survey of relevant sources.

The olfactory ratios of extant avian taxa were collected from data previously published by Bang and Cobb (1968) and Bang (1971). Olfactory ratios were averaged in those species that were included in both studies, though differences between the two sources were minimal. The olfactory ratios of non-avian theropods were drawn from the data published by Zelenitsky et al. (2009, 2011). Preference was given to the more recent data when olfactory ratio measurements conflicted between these sources. For example, the average olfactory ratio of *Allosaurus fragilis* was taken from Zelenitsky et al. (2011) as this study sampled an additional specimen along with the two previously sampled by Zelenitsky et al. (2009). These sources were combined to create a data set of extant avian taxa, consisting of 122 species from more than twenty separate orders and a data set of non-avian theropods, consisting of 22 extinct species from seven distinct theropod taxa. In many cases, the taxonomic placement of a species has changed in the decades since Bang and Cobb (1968) and Bang (1971) published their work. Consequently, genus names were revised to those that are currently accepted. The preponderance of this work was completed using the works of Dunning (2008), Clements et al. (2012), and the IUCN Red List of Threatened Species (all additional sources are provided in Appendix 1).

Many early studies neglected to control for the potentially confounding effects of body size (e.g., Bang, 1971). In an effort to control for this, the average masses of avian species were collected in addition to ecological variables. Average mass data were collected from Dunning (2008). Because neither Bang and Cobb (1968) nor Bang (1971) provided the sexes of the individuals from which their ratios were calculated the masses

of both sexes were averaged when they were provided by Dunning (2008). This includes sexually dimorphic species. When no average mass was given, the maximum and minimum masses of a species were averaged. The masses of subspecies and subpopulations of each species were averaged unless we were able to confidently identify the subspecies or subpopulation from which the olfactory ratio data were drawn. Only Bang (1971) provided the geographic region of specimens. None of the averages calculated herein were weighted by sample size. Predicted masses of non-avian theropod species were collected from Zelenitsky et al. (2009, 2011). These sources did not conflict and consequently, no averages were calculated.

The mating behavior of extant aves was described via a classification of mating system and of pair bond length. Mating system was classified using a five point classification scheme modified from Dunn et al. (2001), in which species were classified as monogamous, mostly monogamous, polygamous, cooperative, or lek/promiscuous. Monogamous taxa were those in which fewer than 5% of the population displayed polygamy, while mostly monogamous taxa were those species in which between 5% and 15% of the population were polygamous (Dunn et al., 2001). In many species, insufficient data existed to distinguish whether a species was monogamous or mostly monogamous. In these cases, species were classified as monogamous (Dunn et al., 2001). Given that traditional estimates suggest that 90% of avian species are monogamous (Ehrlich et al., 1988), this was considered a conservative approach. Polygamous species included both polygynous and polyandrous species and were those species in which less than 85% of the population was monogamous (Dunn et al., 2001). Species that maintained monogamous pair bonds but showed pronounced cooperative breeding

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behavior (e.g., the common moorhen, *Gallinula chloropus*) were classified as cooperative. Mating system data were largely complied from Ehrlich et al. (1988, 1994), Cramp et al. (1977-1994), and Poole et al. (1992-2002) with additional data collected from other previously published works (all additional sources are provided in Appendix 1). Mating system data were collected for a total of 90 species.

Pair bond length was recorded via classifying species as either long-term pair bonding or short-term pair bonding. Species classified as long-term pair bonding were those which typically maintained monogamous pair bonds for two or more consecutive breeding seasons, while species classified as short-term pair bonding were those who did not typically maintain pair bonds over consecutive breeding seasons. Data on pair bond length were primarily collected from Cramp et al. (1977-1994) and Poole et al. (1992-2002) with additional data collected from several other published works (Appendix 1). Pair bond length data were collected for a total of 70 species.

Event timing was classified following Healey and Guilford (1990), in which species were classified as either nocturnal/crepuscular or diurnal. Species were classified as nocturnal/crepuscular if at any point in their life history they displayed nocturnal or crepuscular activity (Healey and Guilford, 1990). Because several predominantly diurnal species are occasionally active in low light conditions (e.g., occasional nocturnal foraging in *Pelecanus occidentalis*, Shields, 2002) event timing data were collected for a conservative diurnal metric and a conservative nocturnal metric. In the former metric, species that occasionally displayed low light activity, but were otherwise predominantly diurnal, were classified as nocturnal/crepuscular, while these species were classified as diurnal under the latter metric. Event timing data were predominantly collected from

Cramp et al. (1977-1994) and Poole et al. (1992-2002) with additional data collected from several other published works (Appendix 1). Event timing data were collected for a total of 91 species.

The migratory and parental care behavior of extant Aves were both classified following Healey and Guilford's (1990) methods. Migratory behavior was accounted for via classifying species as resident (all populations resident), migratory (all populations migratory), or partially migratory (some populations migratory, including dispersive species). Species were also classified as producing either precocial or altricial young, as a proxy for levels of parental care. A final proxy for parental behavior was collected in recording the sex of parents which incubated eggs. Data for all three behaviors were primarily collected from Cramp et al. (1977-1994) and Poole et al. (1992-2002) with additional data collected from other sources. Migratory and incubatory data were collected for 85 species, while hatchling condition was collected for 82 species.

Diet was classified using a modified version of the classification scheme devised by Bang (1971). Bang (1971) classified species as carnivorous (including piscivorous taxa), herbivorous (including frugivorous taxa), insectivorous, granivorous, or polyphagous. Previous authors have suggested that the enlarged olfactory bulbs of the extinct coelurosaurian theropod *Tyrannosaurus rex* (Fig 2) may have been an adaptation used in the location of carrion (Horner and Dobb, 1997 in Zelenitsky et al., 2009). To test this hypothesis, a separate scavenging category was added to those used by Bang (1971) to describe diet. Species were classified as scavenging if carrion accounted for a substantial portion of their diet. Diet was largely collected from Ehrlich et al. (1988, 1994), Cramp et al. (1977-1994), and Poole et al. (1992-2002) with additional data

collected from other previously published sources. Diet was classified for a total of 94 species.

The confounding effects of phylogenetic relations impact all comparative studies, rendering their conclusions questionable if phylogeny is not adequately accounted for (Felsenstein, 1985). Due to species' shared evolutionary history they do not represent independent entries and which do not include some phylogenetic information fail to account for this non-independence (Felsenstein, 1985; Healey and Guilford, 1990). The use of phylogenetic comparative methods to combat the non-independence imposed by taxonomic associations has increased dramatically since the 1980s. There are many methods of varying complexity that can be used to account for these confounding effects (e.g., Felsenstein, 1985; Pagel, 1998). In an effort to control for phylogenetic non-independence, correlations between olfactory ratio and predictor variables were analyzed using phylogenetic generalized least squares (PGLS). PGLS tests each employed 2000 trees, which were constructed from two previously published phylogenies (Ericson et al., 2006; Hackett et al., 2008) and downloaded from birdtree.org (Jetz et al., 2012). Two thousand iterations of PGLS, each employing a different phylogeny, were then completed. Half of these iterations employed phylogenies based upon Ericson et al. (2006) and the other half employed phylogenies based upon Hackett et al. (2008). Models were run using a script (Hunt, personal communication, 2013) for the caper package of R (v. 2.15.2), the code for which is provided in Appendix 2.

Results:

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Olfactory Ratio and Body Mass- Olfactory ratios showed a wide range of values in both non-avian theropods and extant Aves. Extant Aves showed a mean olfactory ratio of 17% with a minimum value of 3% (*Parus atricapillus*) and a maximum of 37% (*Pagodroma nivea*). In general the olfactory ratios of non-avian theropods were significantly higher than those of extant Aves. Non-avian theropods had a mean olfactory ratio of 44.7% with a maximum of 71% (*Albertosaurus sarcophagus*) and a minimum of 27% (*Dilong paradoxus*). A histogram of the olfactory ratios of both groups is shown in Figure 7. Body mass also varied substantially in both groups. Body mass in extant birds ranged from 9.0 grams (*Nectarinia zeylonica*) to 32,400 grams (*Dromaius novaehollandiae*) with a mean mass of 1,084.1 grams. Overall, body mass estimates for non-avian theropods were much higher than those of extant Aves, with a mean
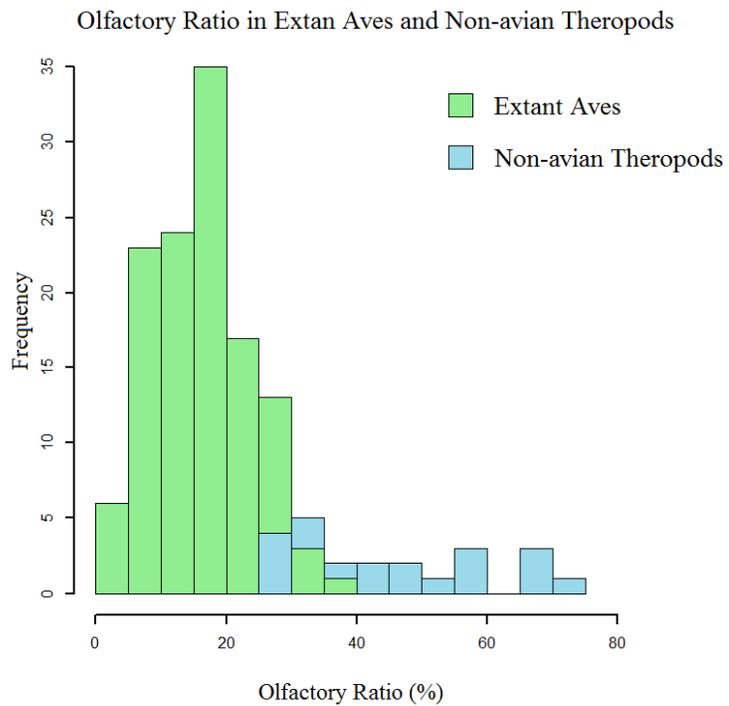
Figure 7: Histogram showing the distribution of olfactory ratios in both extant Aves and non-avian theropods.

body mass of 1667.8 kilograms for the group. As in extant Aves, body mass estimates varied substantially with a minimum value of 2.4 kilograms (*Bambiraptor feinbergi*) and a maximum value of 7905.5 kilograms (*Charcharodontosaurus saharicus*). A histogram

of body mass estimates for both extant Aves and non-avian theropods is shown in Figure 8.

Body Mass of Extant Aves and Non-avian Theropods
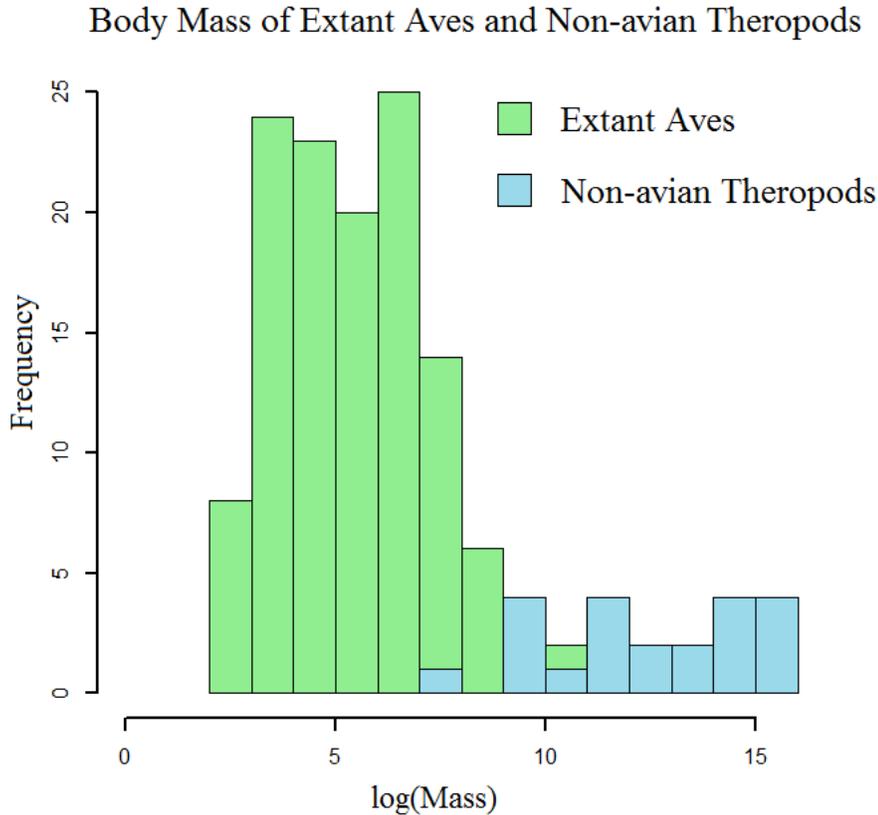
Figure 8: Histogram showing the distribution of body mass in both extant birds and non-avian theropods. Body mass (in grams) has been log transformed.

Iterative PGLS- Phylogenetic generalized least squares tests (PGLS) were conducted to assess the primary effects of each predictor variable. Each model went through 2000 iterations, each time using a different phylogenetic tree. The first 1000 trees employed Ericson et al.'s (2006) phylogeny as a backbone, while the second 1000 trees employed Hackett et al.'s (2008) phylogenetic tree.

Mass was shown to have a weak negative correlation to olfactory ratio in tests employing trees from both backbones. A mean coefficient of -0.52 was returned for trees

based upon Ericson et al.'s (2006) phylogeny and a mean coefficient of -0.51 was

returned for trees based upon Hackett et al.'s (2008) phylogeny (Fig 9). However, of the

2000 PGLS iterations testing for a correlation between olfactory ratio and mass, with no

other independent variables included, only 171 (8.6% of tests) returned p-values of 0.05

or lower. The median p-value for tests using phylogenetic trees based upon Ericson et al.

(2006) was 0.196 while the median p-value for tests using phylogenetic trees based upon

Hackett et al. (2008) was 0.171. Subsequent PGLS analyses which included the effects of

mass also suggested a weak, negative correlation with olfactory ratio. However, as in

models which included body mass as the only predictor variable for olfactory ratio,

relatively few iteration returned p-values that were less than or equal to 0.05.

Of the 2000 iterations that tested models which included mating system as a

predictor variable, none returned p-values which were less than or equal to 0.05. Median

p-values ranged from 0.33 (returned for a monogamous mating system) to 0.75

(polygamous) in models employing phylogenies based upon Ericson et al. (2006) and

ranged from 0.31 (monogamous) to 0.70 (polygamous) in models employing phylogenies

based upon Hackett et al. (2008). Median p-values of 0.18 and 0.15 (Ericson and Hackett

respectively) were returned for the effect of body mass in these models, with a total of

195 (9.8%) iterations returning values less than 0.05. The mean beta values returned from

these models ranged from -2.08 (promiscuous) to 2.12 (mostly monogamous) in Ericson

et al. (2006) models and ranged from -1.94 (promiscuous) to 2.29 (mostly monogamous)

in Hackett et al. (2008) models (Fig 9). As in previous models, a weak negative

correlation between olfactory ratio and mass was recovered. PGLS tests showed that

short term pair bonding species tended to have slightly lower olfactory ratios on average

than their long term pair bonding counterparts (1.75% and 1.73% lower in Ericson and Hackett models respectively). The median p-value for the effect of pair bond length, in models employing phylogenies based upon both Hackett et al. (2008) and Ericson et al. (2006), was 0.22. P-values were less than or equal to 0.05 in 14 iterations (0.7%). Though a weakly negative correlation between mass and olfactory ratio was again recovered, the median p-values for this effect were 0.46 (Ericson) and 0.39 (Hackett), with none of the iterations returning p-values less than or equal to 0.05.

On average low light active species were shown to have olfactory ratios less than 1% higher than their diurnal counterparts. Mean beta values, for this correlation were 0.58 and 0.53 in models based upon Ericson et al. (2006) and Hackett et al. (2008) respectively (Fig 9). Furthermore, only 23 iterations (1.1%) returned p-values less than or equal to 0.05 for the primary effect of event timing on olfactory ratio, with median p-values of 0.52 (Ericson) and 0.57 (Hackett). The effect of mass again showed a weakly negative correlation with olfactory ratio and returned median p-values of 0.13 (Ericson) and 0.11 (Hackett), with 258 (14%) tests returning p-values less than or equal to 0.05. Due to an unknown error, only 1923 iterations could be completed for models including the primary effects of event timing and mass. Despite this, these results are considered to be robust and neither variable was considered to be strongly correlated to olfactory ratio.

The primary effect of migratory behavior showed a weakly positive relationship between olfactory ratio and partial migrant species and weakly negative relationship between olfactory ratio and resident species (Fig 9). Mean beta values returned for the correlation between olfactory ratio and partial migrants were 0.21 and 0.24 in models based upon Ericson et al. (2006) and Hackett et al. (2008) respectively. Median p-values

for this relationship were 0.84 (Ericson) and 0.82 (Hackett). The mean beta values for the

correlation between olfactory ratio and resident species was -2.10 in both models, with

median p-values of 0.23 in those models based upon Ericson et al. (2006) and 0.22 for

those based upon Hackett et al. (2008). Of the 2000 iterations none returned p-values

which were less than or equal to 0.05. As in previous models, a weak negative correlation

between olfactory ratio and body mass was returned, however no iterations returned p-

values less than or equal to 0.05, median p-values were 0.45 (Ericson) and 0.39 (Hackett).

Models including hatchling condition as a predictor variable returned a moderate

positive correlation between altricial young and olfactory ratio. The mean beta value for

this correlation was 3.65 and 3.87 in models employing phylogenies based upon Ericson

et al. (2006) and Hackett et al. (2008) respectively. Median p-values for the effect of

hatchling condition were 0.16 and 0.12 respectively. No iteration, in models using either

phylogenetic backbone, returned a p-value for this effect which was less than or equal

0.05. As in previous models, a weak negative correlation between olfactory ratio and

body mass was returned, however no iterations returned p-values less than or equal to

0.05, median p-values were 0.43 (Ericson) and 0.34 (Hackett). Sex of incubator also

showed a moderate correlation with olfactory ratio, suggesting that species in which only

females brood, and brood parasites, had lower olfactory ratios than species in which both

parents shared incubating duties. Beta values in Ericson models were -2.40 and -3.36, for

female only incubators and brood parasites respectively. In Hackett models, beta values

were -2.27 and -3.25 respectively. As in hatchling condition models, none of the

iterations testing incubatory behavior returned p-values that were less than or equal to

0.05. Median p-values for Ericson models were 0.15 and 0.27, for female only incubators

and brood parasites respectively, and 0.17 and 0.28 for Hackett models. Results returned

for mass were comparable to those returned in hatchling condition models, with mean

beta values of -0.31 (Ericson) and -0.35 (Hackett) and median p-values of 0.52 (Ericson)

and 0.45 (Hackett). No iterations returned p-values less than or equal to 0.05.
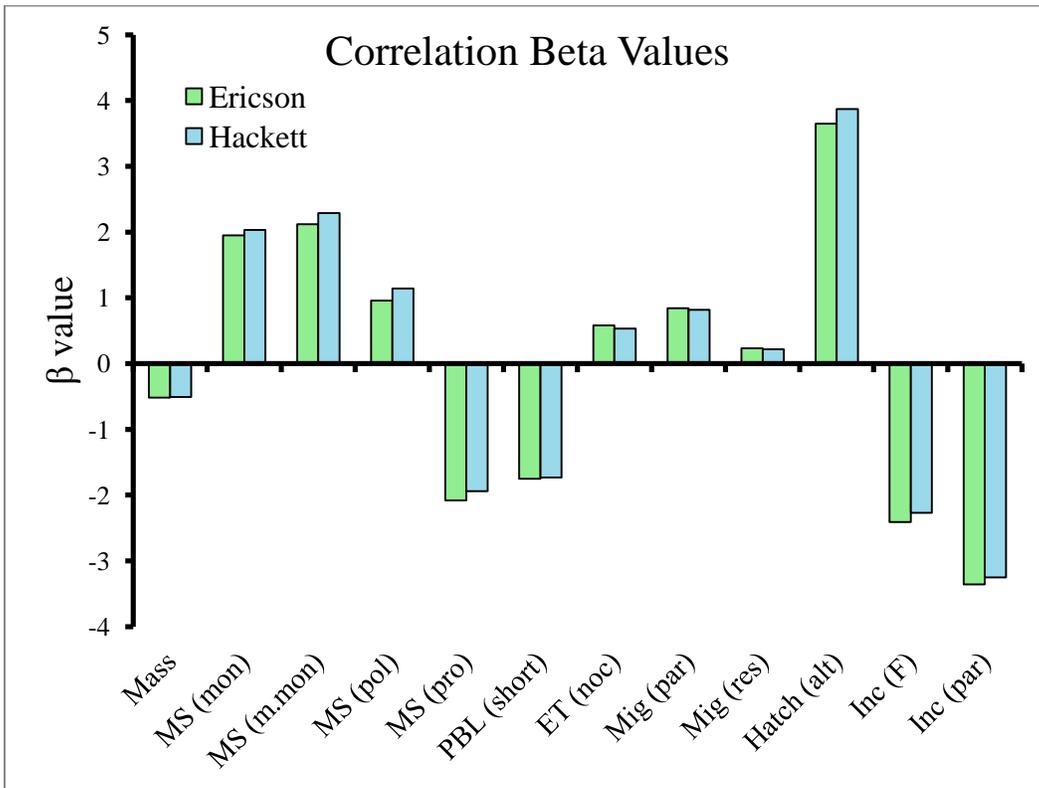
Figure 9: Bar plot showing the mean beta values for correlation between olfactory ratio and the predictor variables of mass, mating system (MS), pair bond length (PBL), event timing (ET), migratory behavior (Mig), hatchling condition (Hatch), and sex of incubator (Inc). Estimates derived from models employing phylogenies based upon Ericson et al. (2006) are in green, while those derived from models employing phylogenies based upon Hackett et al. (2008) are in blue. Beta value estimates for mating system models are shown for monogamous (mon), mostly monogamous (m.mon), polygamous (pol), and promiscuous (pro) taxa and are relative to cooperative breeders. Beta value estimates from migratory behavior models are shown for partial migrant (par) and resident (res) taxa, and are in relation to olfactory ratio values of full migrants. Estimates from models testing incubatory behavior are shown for female only brooders (F) and brood parasites (par), in relation to species where incubation duties are shared by both sexes.

For models testing the primary effects of mass, mating system, pair bond length, event timing, migratory behavior, hatchling condition, and sex of incubator, the phylogenies of Ericson et al. (2006) and Hackett et al. (2008) appear to return negligibly different results in PGLS analysis.

PGLS analysis of the primary effect of diet yielded mixed results. Models employing trees based upon Ericson et al.'s (2006) phylogeny returned positive correlations between olfactory ration and the diet categories of herbivory, insectivory, and scavenging (Fig 10). The magnitude of this correlation varied, with beta values of 2.91, 4.77, and 7.24 for herbivores, insectivores, and scavengers respectively. Similar correlations were returned from models employing trees based upon the phylogeny of Hackett et al. (2008), with beta values of 2.17, 4.23, and 7.40 respectively (Fig 10). Both models also recovered a strong negative correlation between granivory and olfactory ratio (beta values of -4.47 and -4.61 for Ericson and Hackett respectively) and a weak negative correlation between omnivory and olfactory ratio (-1.13 and -1.18 for Ericson and Hackett respectively). The median p-values for these correlations were generally high for all diet groups except for insectivory. Median p-values for the effect of insectivory on olfactory ratio were 0.04 and 0.07 in Ericson and Hackett models respectively. By contrast the median p-values of the remaining diet categories ranged from a maximum of 0.41 (polyphagy) to a minimum of 0.21 (scavenging) in models employing phylogenies based upon Ericson et al. (2006) and ranged from a maximum of 0.52 (herbivory) to a minimum of 0.21 (scavenging) in models employing phylogenies based upon Hacket et al. (2008). In models based upon Ericson et al. (2006), 74.1% of iterations returned p-values less than or equal to 0.05 while only 8% of iterations did so in models based upon

Hackett et al. (2008). Two iterations (0.1 %) returned p-values less than 0.05 for the negative correlation between granivory and olfactory ratio. No other variables returned p-values less than or equal to 0.05 in any iteration. Mass was again found to have a weak negative correlation with olfactory ratio in these models (-0.27 and -0.32 for Ericson and Hackett respectively) but median p-values were high, as in previous models.
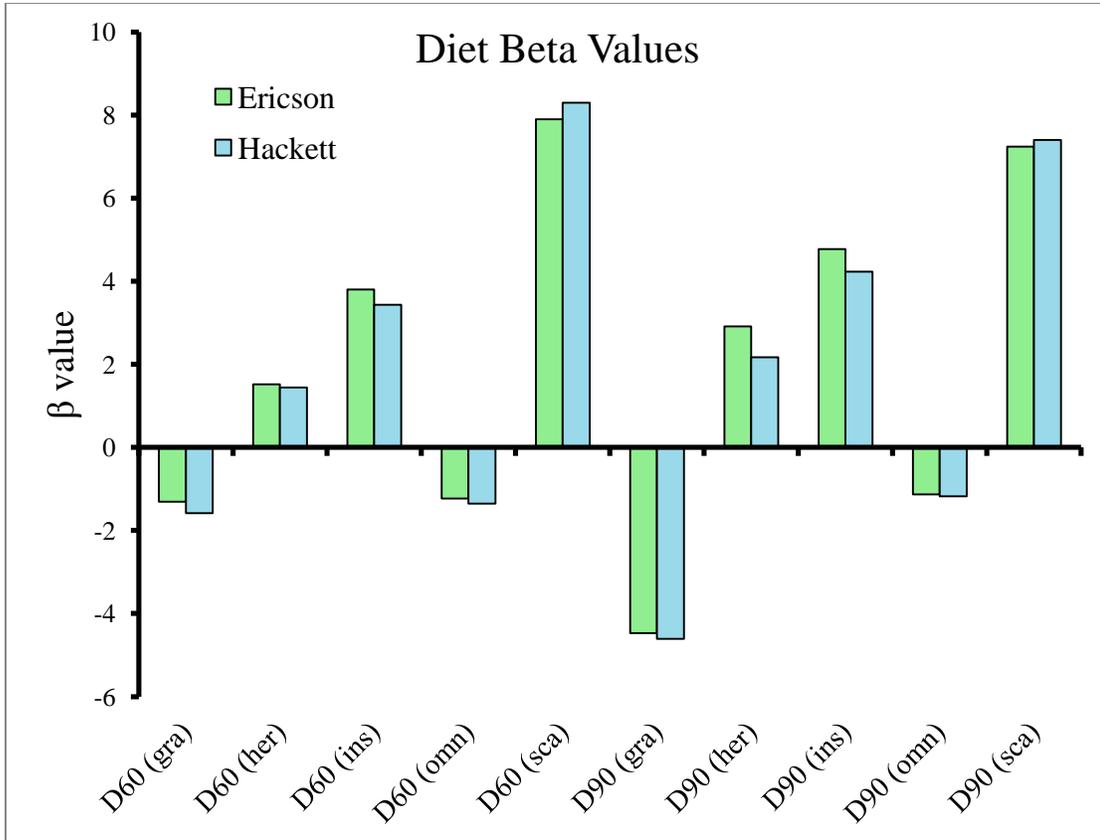
Figure 10: Bar plot showing mean beta values of different diet categories (gra-granivorous, her- herbivorous, ins- insectivorous, omn- omnivorous/polyphagous) in models based upon Ericson et al. (2006) and Hackett et al. (2008). Beta values are presented for both diet classification categories (D60- 60% classification scheme, D90- 90% classification scheme) and are relative to olfactory ratio estimates of carnivorous species.

Diet was initially classified using a conservative method whereby 90% of a species' diet had to be consistent with the dietary group that it was placed in (i.e.,

insectivorous taxa had a diet consisting of 90% insects). This method favored carnivorous and polyphagous taxa, while limiting the number of species which were classified as insectivorous, granivorous, and herbivorous. In an effort to explore the possible confounding effects that such a classification scheme could have had on prior analyses, diet was reclassified using a less conservative 60% cutoff. Under this scheme a species was classified as insectivorous if 60% or more of its diet consisted of insects. Models employing this less conservative classification of diet yielded similar results to previous models, with some exceptions (Fig 10). Beta values changed only slightly in most cases, though the strength of the correlation between granivory and olfactory ratio was substantially reduced, with beta values increasing from -4.47 to -1.31 in models based upon Ericson et al. (2006) and increasing from -4.61 to -1.58 in models based upon Hackett et al. (2008). The magnitude of the correlation between olfactory ratio and an insectivorous diet was also slightly reduced (Figure 10, Table 1).

	Insects 90% of Diet		Insects 60% of Diet	
	β	%	β	%
Ericson et al. (2006)	4.77	74.1	3.81	22.6
Hackett et al. (2008)	4.23	8.0	3.43	2.4

Table 1: Table summarizing effect of an insectivorous diet on olfactory ratio in PGLS models employing two different methods for classifying diet. The percent of iterations which returned p-values less than or equal to 0.05 and the mean beta values are presented.

Median p-values and the number of iterations which returned p-values less than or equal to 0.05 were also changed only slightly. For example, the median p-value for the effect of insectivory increased from 0.04 to 0.06 in models based upon Ericson et al. (2006) and from 0.07 to 0.09 in models based upon Hackett et al. (2008).

However, the number of iterations returning p-values less than or equal to 0.05 did decrease substantially for the effect of insectivory, a trend that is especially pronounced in models employing phylogenies based upon Ericson et al. (2006) (Table 1).

Discussion:

All the models tested herein suggested that mass was not strongly correlated to olfactory ratio. Additionally, because each model tested a different number of species (dictated by the number of species for which data could be collected for each individual ecological variable), it would appear that this result is not sensitive to the effects of sample size. These results contradict those found by other authors, namely Healey and Guilford (1990), who found that mass explained nearly 50% of the variation in avian olfactory bulb size. The discrepancy between the data presented herein and that presented by Healey and Guilford (1990) can potentially be explained by the fact that Healey and Guilford used olfactory bulb size rather than olfactory ratio. Standardization of olfactory bulb size, via the calculation of olfactory ratios, thus appears to largely account for the potentially confounding effects of body size. The weak correlation of olfactory ratio and mass, recovered in this study, may also be contingent upon the inclusion of phylogenetic data, as preliminary multiple regressions (Brightly and Lockwood, unpublished data) returned significant results for the effect of mass in some cases. Thus it appears that the use of olfactory ratios, in conjunction with some variable accounting for phylogeny, satisfactorily controls for the potentially confounding effects of body size.

The ability to control for body size in this way is potentially useful to the study of olfaction in non-avian theropods for a number of reasons. First, because the brains of non-maniraptoriform theropods were not in contact with the braincase, reliable estimates of the dimensions of their olfactory lobes cannot be calculated from endocasts (Zelenitsky et al., 2009, 2011). However, olfactory ratios can be accurately calculated for non-maniraptoriform theropod species because the ratio between the different portions of the endocranial cavity is assumed to accurately represent the ratio between the soft parts which they originally housed (Larsson et al., 2000; Zelenitsky et al., 2009, 2011). Thus, a model employing olfactory lobe size and body mass, as in Healey and Guilford (1990), could not realistically be applied to many non-avian theropod species. A second potential benefit of this method for controlling for body size is that it does not require mass estimates of extinct theropod species. Body mass estimates in non-avian theropods vary substantially as there is no standardized method for estimating body mass and many estimates are made from largely incomplete specimens (e.g., Farlow et al., 1995; Christiansen and Farina, 2004; Therrien and Henderson, 2007). Body mass estimates of the charismatic theropod species, *Tyrannosaurus rex*, vary by more than 2500 kilograms in the literature (e.g., Farlow et al., 1995; Therrien and Henderson, 2007). Indeed this range is so great that the weight of two *Allosaurus fragilis* could be subtracted from maximum estimates and they would still be larger than minimum estimates (Farlow et al., 1995; Therrien and Henderson, 2007). Thus the benefits of a model which does not require body mass estimates could be crucial to the comparative study of olfaction in non-avian theropods. However, if the adequate control of body size, in the absence of body mass estimates, requires the incorporation of phylogenetic data this model may

prove less attractive, as parts of the theropod phylogenetic tree remain poorly resolved (Holtz, 2004). Furthermore olfactory ratio alone may prove to be an insufficient control for body size in animals which grew to sizes which were orders of magnitude larger than extant Aves. Ultimately, further research is needed in this area in order to determine the most accurate method for controlling for the potentially confounding effects of body size in non-avian theropods.

Apart from body size, there are several other variables which may confound reconstructions of olfactory acuity, in both extant Aves and non-avian theropods. One potential source of error is cerebral hemisphere morphology. Indeed it is possible that changes in olfactory ratio are not necessarily linked to changes in the size of the olfactory lobes, but rather are the result of changes in cerebral hemisphere morphology. This potential confounding variable has not been controlled for herein, and future work should ideally take this into account as a potential source of error. Additionally, this study has made no efforts to control for the potentially confounding effects of allometry. Allometric growth of the olfactory lobes could potentially have a large impact upon the results presented herein and future work should take this variable into account. Ultimately more work is needed to fully understand the impacts that body size, brain size, and allometric growth have upon olfactory lobe morphology.

The results of this study suggest that the ecological variables of mating system, pair bond length, migratory behavior, hatchling condition, incubator sex, and event timing are not strongly correlated with olfactory acuity when the effects of phylogeny are sufficiently controlled for. In general the beta values for the correlation between these variables and olfactory ratio was quite low. Several variables had mean beta values that

suggested slightly higher magnitude of correlation to olfactory ratio (i.e., hatchling condition and sex of incubator, Fig 9) but these universally had very high median p-values and few iterations which returned p-values which were less than or equal to 0.05. Of particular interest among these variables is event timing. Healey and Guilford (1990) found a correlation between olfactory lobe size and event timing in modern birds, which remained significant even once phylogeny and body size had been controlled for. This correlation showed that nocturnal and crepuscular species tended to have higher olfactory ratios and thus increased olfactory acuity (Healey and Guilford, 1990). The authors intuitively explained this increased olfactory acuity as a response meant to compensate for the reduced effectiveness of vision under low light conditions (Healey and Guilford, 1990). The results of this comparative analysis have even been extended to the fossil record. Zelenitsky et al. (2009) calculated the olfactory ratios of several extinct theropod species and hypothesized that the enlarged olfactory lobes of both tyrannosaursids and dromaeosaursids could potentially have been an adaptation to low light activity.

The results presented herein directly contradict those presented by Healey and Guilford (1990). PGLS tests returned an exceedingly small difference between the average olfactory ratios of diurnal and low light active species and median p-values associated with this correlation were quite high. The probable explanation for the disparity between our results and those presented by Healey and Guilford is the method in which phylogenetic non-independence was controlled for in each analysis. While Healey and Guilford (1990) employed a family level analysis, the present study employed the much more robust method of phylogenetic generalized least squares. Thus, it is suggested that the significant correlation between olfactory lobe size and event

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timing recovered by Healey and Guilford (1990) was merely an artifact of inadequate control for phylogenetic non-independence. Indeed, preliminary multiple regressions which did not control for phylogenetic non-independence also returned significant results for the effect of event timing on olfactory ratio. Furthermore it is suggested that olfactory ratio is an inadequate proxy for studying event timing in non-avian theropods.

The strongest correlation uncovered in the present study was between diet and olfactory ratio. Results suggested that insectivorous taxa tended to have increased olfactory ratios compared to their non-insectivorous counterparts. However the results were highly dependent upon a number of variables. The first factor affecting the correlation between olfactory ratio and insectivory was the manner in which diet was classified. Diet was originally classified using a conservative approach whereby the diet of a species was required to consist of at least 90% insects in order to be classified as insectivorous. This classification scheme restricted insectivorous diet, in addition to other specialist diet categories, to only a handful of species and was seen as being overly conservative. Thus diet was reclassified using the less conservative cutoff of 60%, rather than 90%. This resulted in a substantial increase in the number of taxa classified as insectivores and also changed the strength of the correlation and the median p-values associated with it. The disparity between the results returned by these two classification schemes potentially reflects an adaptive advantage to increased olfactory acuity in obligate insectivores which is not shared by those species which have wider access to, or ability to exploit alternate food sources. However the different results between these two classification schemes could also be the result of the confounding effects of small sample

size. An expanded dataset testing both diet classification schemes could potentially reveal the cause of this phenomenon.

The second factor affecting the correlation between olfactory ratio and insectivorous diet was the phylogenetic backbone which was used during PGLS tests. In both classification schemes, median p-values were higher and substantially fewer iterations returned p-values less than or equal to 0.05 in PGLS tests employing trees based upon the phylogeny of Hackett et al. (2008). The main difference between the phylogenies of Hackett et al. (2008) and Ericson et al. (2006) is the inclusion or exclusion of the β-fibrinogen gene, which has a large impact upon the topology of upper-level avian phylogeny (Jetz et al., 2012). Molecular phylogenies which exclude β-fibrinogen from their analysis do not recognize the Metaves (one of the two proposed divisions within Neoaves) as a monophyletic clade, while those studies which include β-fibrinogen do (Jetz et al., 2012). The seventh intron of the β-fibrinogen gene is purported to contain a large number of indels, whose presence pose a significant barrier to accurate sequence alignment (Morgan-Richards et al., 2008; Jetz et al., 2012). Thus, the recovery of a monophyletic Metavian clade is potentially linked to misalignment of the β-fibrinogen gene (Morgan-Richards et al., 2008; Jetz et al., 2012). Of the phylogenies used in the present study, Ericson et al. (2006) excluded β-fibrinogen from their analysis, while Hackett et al. (2008) included the gene (Jetz et al., 2012). Thus, models which returned higher beta values and lower median p-values were free from the potentially confounding effects of faulty β-fibrinogen alignment. However favoring these results over those recovered by models employing trees based upon Hackett et al. (2008) is considered premature at this time, as the full extent of the phylogenetic effects of the inclusion or

exclusion of the β-fibrinogen gene is not fully understood (Jetz et al., 2012). Furthermore there was no appreciable difference between phylogenies in the results returned for any other ecological variable examined in this study.

The explanation for why increased olfactory acuity could be an adaptive advantage to insectivorous Aves remains largely unclear. Though some evidence suggests that olfactory cues may be important in the foraging of birds (e.g., Wenzel, 1971) research which connects olfactory cues to insectivorous foraging is scarce. However, there is a substantial body of work which suggests that odors may be important components in the aposematic warnings of many toxic insects (Roper, 1999). In aposematic insect species, chemical cues often times accompany bright coloration and may serve as a deterrent which birds may respond to (Roper, 1999). Rowe and Guilford (1996) showed that pyrazines (a chemical cue common to many toxic insects; Roper, 1999; Roper and Guilford, 1996), induced an aversion to yellow and red food in domestic chicks, but did not induce an aversion to green food. Furthermore no aversion was observed in the absence of pyrazines, regardless of coloration (Rowe and Guilford, 1996). These results thus suggest that chemical cues play a critical role in the recognition and avoidance of toxic insects in domestic chicks. Similar results were returned by Marples et al. (1994) who showed that the aversion response of Japanese quail to the combined factors of color pattern, taste, and scent was significantly higher than the aversion response to any single cue or pair of cues. However, the individual effect of scent was low and the paired effects of color and scent resulted in lower levels of aversion than were recorded for color alone (Marples et al., 1994). The authors thus hypothesized that

scent, in the absence of the remaining aposematic cues, could act as an attractor in Japanese quail (Marples et al., 1994).

The ability to better detect aposematic cues, by virtue of increased olfactory acuity, could potentially be an adaptive advantage for insectivorous taxa. Species that primarily consume insects would presumably encounter toxic insects more frequently than those species for which insects are rarely consumed. Thus, if increased olfactory acuity allows for better recognition of these toxic species it is presumed that evolutionary pressure would push species towards increased olfactory acuity and thus higher olfactory ratios. Furthermore, if the attractor hypothesis of Marples et al. (1994) is true, individuals which can better detect these cues would have the clear benefit of increased access to food (assuming the insects in question are not toxic and thus other aposematic cues are not present) relative to their conspecifics. In this scenario, selection should again favor higher olfactory acuity. However, this field is still poorly understood and further research into the connection between insectivory and olfactory cues is needed before any conclusions can be confidently drawn.

Even if the correlation between diet and olfactory ratio is accepted for extant Aves, drawing conclusions about insectivorous diet in non-avian theropods, based upon olfactory ratio, is problematic for a number of reasons. Insectivorous diet has only been suggested for a small number of theropods and, to the best of our knowledge, the evidence these hypotheses are based upon is entirely indirect (e.g., Senter, 2004). Several authors have suggested that the alvarezsaurs, a clade of small theropods, were insectivores who used their unique, stunted forelimbs to dig termite hills (e.g., Senter, 2004; Longrich and Currie, 2009). Senter (2004) examined the range of forelimb

movement which the alvarezsaurs *Mononykus olecranus* was capable of and concluded

that the species was incapable of burrowing or using its forelimbs to grasp prey in the

usual theropod fashion. However, the range of movement which *Mononykus olecranus*

was capable of allowed it use hook-and-pull movements, a behavior practiced by extant

anteaters, pangolins, and armadillos to dig termite nests (Senter, 2004). In addition many

of these extant taxa possess a single enlarged manual digit, a condition which *Mononykus*

olecranus also possessed (Senter, 2004). Alvarezsaurs also expressed several other traits

consistent with a myrmecophagous diet (ants, termites, and other colonial insects)

including reduced and simplified teeth, weak mandibles, and narrow jaws (Longrich and

Currie, 2009). However, the probable insectivorous diet of alvarezsaurs was paired with

relatively small olfactory bulbs (Alifanov and Saveliev, 2011). X-ray sections of a natural

brain endocast of *Ceratonykus oculatus* revealed substantially smaller olfactory bulbs

than many extant reptiles; a trait which the authors suggest may be related to a decrease

in the functional significance of the olfactory system (Alifanov and Saveliev, 2011).

Though there is some indication that *Ceratonykus oculatus* may have had some

specialization of secondary olfactory centers (Alifanov and Saveliev, 2011), there is no

indication that it shared the olfactory specialization which extant insectivorous Aves

appear to have possessed.

There is also some evidence that the Troodontidae may have had an insectivorous

diet. The dentition of the Troodontidae differed substantially from that of other

contemporary theropods (Varricchio, 1997). In general, troodontids had very high tooth

counts and large denticles which curved towards the tips of their teeth (Varricchio, 1997).

This morphology resulted in a high number of sharp cusps, a condition which is also

found in several extant insectivores such as the bat-eared fox (Varricchio, 1997). However, as in alvarezsaurs, this morphology is not accompanied by enlarged olfactory bulbs (Zelenitsky et al., 2009; 2011). Indeed, *Troodon formosus* has an olfactory ratio more than 10% lower than that of the theropod mean (calculated from the 22 species included in Zelenitsky et al., 2009; 2011) and nearly 8% below that of *Deinonychus antirrhopus* which is of similar size (Zelenitsky et al., 2009; 2011). Thus the troodontidae also appear to directly contradict the trend of increased olfactory ratio found in extant insectivorous birds. Furthermore, there is no evidence to suggest an insectivorous diet for those species which do have enlarged olfactory bulbs. The tyrannosaurs all possess large olfactory bulbs, even when body mass is taken into account (Zelenitsky et al., 2009; 2011). However their large size seems to preclude them from possessing a largely insectivorous diet. Size would not necessarily preclude many members of Dromaeosauridae, who also possess relatively large olfactory lobes, from an insectivorous diet; however, their dentition does not suggest any diet other than strictly carnivorous (Currie, 1997).

Conclusion:

Many of the variables correlated to olfactory ratio by previous authors are not supported when more robust, modern methods for controlling for phylogenetic non-independence are applied. Chief among these are body mass and event timing. The results presented herein suggest that the confounding effects of body size are largely controlled for by using olfactory ratio, though phylogenetic control may also be

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necessary. The effect of event timing does not remain a strong predictor of olfactory ratio under PGLS analysis and it is suggested that the work of Healey and Guilford (1990) likely suffered from the inadequate control of phylogenetic non-independence. Though a results suggest that there is potentially a real correlation between olfactory ratio and an insectivorous diet in extant Aves, the large dependence of these effects on phylogeny and diet classification suggest that olfactory ratio is not an effective proxy for insectivory in extant Aves. This fact, coupled with several other factors suggests that olfactory ratio is not an effective proxy for this suite of ecological variables, in non-avian theropods.

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APPENDIX II: R Code for Iterative PGLS Models

Load Data:
```
Aves<-read.csv(file=file.choose())
trees<- read.nexus(file=file.choose())
```

Set Parameters:
```
num.trees<-length(trees)
pgls.result<-list()
```

Run Iterative Model:
```
for(i in 1:num.trees){
 focal.tree<-trees[[i]]
 Phy<-comparative.data(phy=focal.tree, data=Aves, Tree_Tip, vcv=TRUE, vcv.dim=3)
 pgls.result[[paste("run",i,sep="")]]<-pgls(OR~log(Mass)+Diet60, Phy)
 }
```

Characterize Results (OR~log[Mass]+Diet):
```
myFun <-function(pgls)
{
out <- c(summary(pgls)$coefficients[,1],
        summary(pgls)$coefficients[,4],
        summary(pgls)$r.squared)
names(out) <-
c("intercept.estimate","intercept.mass","intercept.gran","intercept.herb","intercept.ins","i
ntercept.poly","intercept.scav","intercept.p.value","mass.p.value","gran.p","herb.p","ins.p
","poly.p","scav.p","mult.r.squared")
return(out)}
```

Results for All Tests:
```
results <- list()
for (i in 1:length(pgls.result)) results[[names(pgls.result)[i]]] <- myFun(pgls.result[[i]])
as.data.frame(results)
```

Save to Excel:
```
WB<-loadWorkbook("Diet60Hackett.xlsx", create=TRUE)
createSheet(WB, names(results))
writeWorksheet(WB,  results, names(results), header=FALSE, rownames=
names(results))
saveWorkbook(WB)
```

APPENDIX III

Species	OR (%)	Mass (g)	Mat. Sys.	PBL	Di. Cons.	Noc. Cons.	Migr.	Diet90	Diet60	Hatch. Cond.	Brooding
Aix sponsa	25.6	658	2	0	Yes	Yes	2	polyphagous	herbivorous	precocial	F
Amandava amandava	10	9.6	2	1?	No	No	1	polyphagous	granivorous	?	B
Amaurornis phoenicurus	23	180									
Anas carolinensis	20	341	2?	0	Yes	Yes	3?	polyphagous	polyphagous	precocial	F
Anas platyrhynchos	19	1141	3	0	Yes	Yes	2	polyphagous	polyphagous	precocial	F
Apteryx australis	34	2330	2	1	Yes						
Apus affinis	18.7	17.9	2	1	Yes	Yes	2	insectiorous	insectivorous	altricial	B
Asio flammeus	19	325	2	0	Yes	Yes	2	carnivorous	carnivorous	altricial	F
Bicanistes subcylidricus	8	1200.5						polyphagous	herbivorous		
Bonasa umbellus	14	532	6	0	Yes	Yes	1	polyphagous	herbivorous	precocial	F
Bubo virginianus	18	1191.25	2	1	Yes	Yes	1	carnivorous	carnivorous	altricial	F
Caprimulgus asiaticus	22	42			Yes			insectivorous	insectivorous		
Caprimulgus vociferus	25	53.4	2	?	Yes	Yes	3	insectivorous	insectivorous	precocial	B
Carpodacus purpureus	4	23.3	2	?	No	No	3?	polyphagous	herbivorous	altricial	B
Cathartes aura	28.7	2006	2	1	Yes	No?	2	scavenger	scavenger	altricial	B
Centropus sinensis	18	283									
Chaetura pelagica	19	23.6	5	?	No	No	3	insectivorous	insectivorous	altricial	B
Charadrius semipalmatus	15	46.75	2	1?	Yes	Yes	3	carnivorous	carnivorous	precocial	B
Cinclus cinclus	10.7	61.7	2	0	No	No	2	carnivorous	insectivorous	altricial	F
Coccothraustes vespertinus	4	57.35	2	?	Yes	No	2	polyphagous	polyphagous	altricial	F
Coccyzus americanus	21	64	2	?	Yes	Yes	3?	insectivorous	insectivorous	altricial	B
Colaptes auratus	8	131.6666667	2	0?	Yes	Yes	2	polyphagous	insectivorous	altricial	B
Columba livia	22	354.5	2	1	Yes	No	1	herbivorous	granivorous	altricial	B
Coracias benghalensis	14	158	2	?	Yes	Yes	3	carnivorous	insectivorous	altricial	F
Coracina melanoptera	12	30									
Coragyps atratus	17	2159	2	1	No?	No	2	scavenger	scavenger	altricial	B
Corvus brachyrhynchos	5	506	5	1	No	No	2	polyphagous	herbivorous	altricial	F

Species											
Cuculus varius	20	103									
Cyanocitta cristata	6	88	2	1	No	No	2	polyphagous	polyphagous	altricial	F
Cypsiurus parvus	18.7	13.6									
Daption capense	27.5	435.5	2	1	Yes	Yes	2	carnivorous	carnivorous	altricial	B
Dendrocitta vagabunda	7	100									
Dicrurus adsimilis	16.2	40.3						carnivorous	insectivorous		
Dromaius novaehollandiae	26.3	34200	1	0	Yes						
Eudynamys scolopaceus	19	200			Yes?						
Falco peregrinus	20	783.3333333	2	1	Yes	Yes	2	carnivorous	carnivorous	altricial	B
Fratercula arctica	13.9	652	2	1	No?	No	2	carnivorous	carnivorous	precocial	B
Fregata magnificens	15	1499.25	2	0	Yes	No	2	carnivorous	carnivorous	altricial	B
Fulica americana	24	642	2	1?	Yes	Yes	2	polyphagous	herbivorous	precocial	B
Fulica atra	25	836	2	1	Yes	Yes	2	polyphagous	herbivorous	precocial	B
Fulmarus glacialis	27	613	2	1	Yes	Yes	2	carnivorous	carnivorous	altricial	B
Gallinago delicata	14	122	3	0	Yes	Yes	2	polyphagous	polyphagous	precocial	F
Gallinula chloropus	20	343.5	5	1	Yes	Yes	2	polyphagous	polyphagous	precocial	B
Gallirallus australis	24	899.3333333	2	1	Yes	Yes	1	polyphagous	herbivorous	precocial	B
Gavia immer	20	4980	2	1	Yes	Yes	3?	carnivorous	carnivorous	precocial	B
Gracula religiosa	8	192									
Haliastur indus	12.5	529	2?								
Hirundo rustica	15	17.98333333	3	1	No	No	3?	insectivorous	insectivorous	altricial	B
Hydrophasianus chirurgus	20	163.5						polyphagous	herbivorous		
Lanius schach	16	51.55			No?						
Larus argentatus	16	1085	2	1	Yes	No	2	carnivorous	carnivorous	precocial	B
Limnodromus griseus	15	110.75	2	?	Yes	Yes	3	polyphagous	carnivorous	precocial	B
Megaceryle alcyon	17	148	2	0	Yes	No	2	carnivorous	carnivorous	altricial	B
Megalaima asiatica	15.4	90.5									
Megalaima haemocephala	9.3	44.55			No?						

Species												
Megascops asio	15.5	180.5		3	1	Yes	Yes	1	carnivorous	carnivorous	altricial	F
Meleagris gallopavo	13.5	6050		4	0	No	No	1	polyphagous	herbivorous	precocial	F
Melopsittacus undulatus	6	28.7										
Mergus serrator	15	1021.5		2	0	Yes	Yes?	3	carnivorous	carnivorous	precocial	F
Merops orientalis	18.7	14.8		2	?	No	No	2	insectivorous	insectivorous	altricial	B
Micropternus brachyurus	14.3	88.2										
Milvus migrans	15	567		2	1	Yes	No	2	carnivorous	carnivorous	altricial	B
Molothrus ater	7	40.68333333		4	0	No	No	3?	polyphagous	granivorous	altricial	N
Motacilla flava	13.6	17.7		2	0	Yes	No	2	insectivorous	insectivorous	altricial	B
Motacilla maderaspatensis	16	30.5										
Nectarinia zeylonica	12.9	9										
Nycticorax nycticorax	20	810		2	0	Yes	Yes	2	carnivorous	carnivorous	altricial	B
Oceanites oceanicus	33	30.45		2	1	Yes						
Oceanodroma leucorhoa	33	36.925		2	1	Yes	Yes	3?	carnivorous	carnivorous	altricial	B
Opisthocomus hoazin	24.2	696		5		Yes			herbivorous	herbivorous		
Oriolus xanthornus	13.25	56.3										
Pachyptila desolata	29.5	147		2	1?	Yes	Yes	2?	carnivorous	carnivorous	altricial	B
Pagodroma nivea	37	268		2	1	Yes	Yes	2	carnivorous	carnivorous	altricial	B
Pandion haliaetus	14	1485.5		2	0?	Yes	No	2	carnivorous	carnivorous	altricial	B
Passer domesticus	4	27.7		2	1	Yes	No	2	granivorous	granivorous	altricial	B
Passerella iliaca	5.5	33.32		2	?	Yes	Yes	3	polyphagous	polyphagous	altricial	F
Pelecanoides georgicus	18	121	2?		?	Yes	?	1?	carnivorous	carnivorous	altricial	B
Pelecanus occidentalis	9.6	3438		2	?	Yes	No	2	carnivorous	carnivorous	altricial	B
Phaethon aethereus	20	750		2	1	No	No	2	carnivorous	carnivorous	altricial	B
Phalacrocorax auritus	10	1817		2	0	No	No	2	carnivorous	carnivorous	altricial	B
Phalacrocorax carbo	14.5	2571.166667		2	1	No	No	2	carnivorous	carnivorous	altricial	B
Phalacrocorax niger	15.8	427	2?		?	No?						
Phalacrocorax pelagicus	8	1856.5		2	0?	Yes	No	2	carnivorous	carnivorous	altricial	B

Species												
Phalacrocorax urile	8	2137.5	2	0?	No?	No		2	carnivorous	carnivorous	altricial	B
Phoebastria nigripes	29	3195	2	1	Yes	No?	3?	carnivorous	carnivorous	precocial	B
Phoeniconaias minor	21.7	1500	2	1?	Yes	Yes	2	polyphagous	herbivorous	precocial	B
Picoides pubescens	10	25.675	2	?	No	No	2	polyphagous	insectivorous	altricial	B
Pitta brachyura	18	55.5						carnivorous	insectivorous		
Podiceps auritus	27	453	2	1	Yes	Yes	3	carnivorous	carnivorous	precocial	B
Poecil atricapillus	3	10.8	2	1	No	No	1?	polyphagous	polyphagous	altricial	F
Polysticta stelleri	23.7	807.5	2	0	Yes	No	3	carnivorous	carnivorous	precocial	F
Porphyrio porphyrio	21	793.5	2 or 5	?	Yes	Yes	2	polyphagous	herbivorous	precocial	B
Porzana fusca	23	57.6						polyphagous	polyphagous		
Psittacula krameri	10	116.5	2	1?	No	No	1	herbivorous	herbivorous	altricial	F
Puffinus gravis	30	849					3				
Puffinus opisthomelas	29	408	2?	?	Yes	Yes	2	carnivorous	carnivorous	altricial	B
Puffinus pacificus	30	388	2	1	Yes	Yes	2	carnivorous	carnivorous	altricial	B
Pygoscelis adeliae	17	4850	2	1	Yes	Yes	2	carnivorous	carnivorous	altricial	B
Quiscalus quiscula	9	106.1	3	0	No	No	2	polyphagous	polyphagous	altricial	F
Rallus elegans	20	318.75	2	?	Yes	Yes	2	polyphagous	carnivorous	precocial	B
Rallus limicola	25.6	84.1	2	0?	Yes	Yes	2	polyphagous	carnivorous	precocial	B
Rallus longirostris	20	262.5	2	0?	Yes	Yes	2	polyphagous	carnivorous	precocial	B
Rhea americana	19	23000	6	0	Yes			polyphagous	polyphagous		
Scolopax minor	17	197.5	4 or 6	0	Yes	Yes	3?	polyphagous	carnivorous	precocial	F
Serinus canaria	6	24.3	2	1?	No	No	1	polyphagous	herbivorous	?	F
Steatornis caripensis	23.25	408	2?		Yes			herbivorous	herbivorous		
Sturnus malabaricus	13	39.6									
Sturnus vulgaris	9.7	78.03333333	3	0	Yes	Yes	2	polyphagous	polyphagous	altricial	B?
Sula bassana	9.6	2999.5	2	1	No	No	2	carnivorous	carnivorous	altricial	B
Tachybaptus ruficollis	22	174	2	1	Yes	Yes	2	carnivorous	carnivorous	precocial	B
Tephrodornis pondicerianus	17.5	20.2									

Treron phoenicopterus	20	235									
Tribonyx mortierii	26	1292.5									
Tribonyx ventralis	24	387	?	?	Yes	No	2	polyphagous	herbivorous	precocial	?
Turdoides caudatus	6	39.65	5	?	No	No	3	polyphagous	polyphagous	?	B
Turdus migratorius	8	78.5	2	0	Yes	No	2	polyphagous	polyphagous	altricial	F
Turnix suscitator	12.5	50.5									
Upupa epops	14.6	67.13333333	2	0	Yes	Yes	2	carnivorous	insectivorous	altricial	F
Uria lomvia	15	964	2	1	Yes	Yes	2	carnivorous	carnivorous	precocial	B
Urocolius macrourus	9.7	45.5									
Vanellus indicus	22	181	2	1	Yes	Yes	2	insectivorous	insectivorous	precocial	B
Zonotrichia albicollis	4.5	24.4	2	1?	Yes	Yes	3	polyphagous	polyphagous	altricial	F