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Ecological Controls on the Campanian Distribution of Hesperornis (Aves: Hesperornithiformes) in the Western Interior Seaway

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ECOLOGICAL CONTROLS ON THE CAMPANIAN DISTRIBUTION OF *HESPERORNIS* (AVES: HESPERORNITHIFORMES) IN THE WESTERN INTERIOR SEAWAY

being

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by

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the Master of Science Degree

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ABSTRACT

The epicontinental Western Interior Seaway (WIS) of Late Cretaceous North America provided a unique marine habitat for cephalopods, fish, marine reptiles, and the foot-propelled diving seabird *Hesperornis*. While several predator-prey relationships among *Hesperornis* or other hesperornithiforms and other WIS animals have been hypothesized based on gut contents, bite marks, and coprolites/colonites, ecological relationships have not been quantitatively tested. Paleontological species distribution modeling (SDM) studies have focused on extinct non-marine taxa and marine invertebrates, with only two marine vertebrate studies of extant taxa. Here, two SDM methods were used to test the influence of vertebrate faunas, sedimentary rock type, paleogeography, and outcrop area on *Hesperornis* occurrences: generalized linear models (GLMs) and occupancy models (an extension of standard GLMs). Results of both model types indicate a decreased probability of *Hesperornis* presence at elasmosaur-occupied sites and an increased probability of *Hesperornis* presence with higher paleolatitudes. The negative association between elasmosaurs and *Hesperornis* in all highest-ranked models, coupled with evidence of similar diets, may indicate food resource competition, but the geographic distributions of both taxa may instead reflect different habitat preferences. The positive impact of paleolatitude may reflect seasonal migrations resulting in large breeding congregations at higher paleolatitudes (based on probable immature specimens), preference for specific environmental conditions or feeding areas (e.g., along oceanographic fronts or upwelling zones), or migration mortality. While Spearman's correlation test did not identify a western, middle, or eastern WIS preference for *Hesperornis*, the inclusion of this regional covariate with paleolatitude in the highest-ranked occupancy models may indicate an interaction effect between these two covariates that favored higher *Hesperornis* abundance in South Dakota and Manitoba along probable mixing zones or fronts. Taxa hypothesized by previous authors to have had ecological interactions with hesperornithiforms were not supported by the models as major factors in the *Hesperornis* distribution. These include *Tylosaurus* and polycotylid plesiosaurs, hypothesized feeders on *Hesperornis*, *Enchodus,* a teleost consumed by the smaller hesperornithiform *Fumicollis,* and *Squalicorax,* an opportunistic shark that consumed hesperornithiforms. This study represents the first paleogeographic model for *Hesperornis* occurrences and the first GLM and occupancy modeling applications to extinct marine vertebrates. These models examine previous hypotheses and provide novel interpretations for hesperornithiform ecology.

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INTRODUCTION

During the Campanian Age of the Late Cretaceous, the epicontinental Western Interior Seaway (WIS) divided North America with water depths of 60 m or more (Gill and Cobban, 1966; Hanczaryk and Gallagher, 2007; Slattery et al., 2018). In addition to fish, marine reptiles, cephalopods and other invertebrates, the WIS was also home to hesperornithiforms (Hesperornithiformes), flightless foot-propelled diving seabirds most comparable to cormorants (Phalacrocoracidae) and diving ducks (*Aythya* and *Mergus*) in hindlimb morphology (Bell et al., 2019). *Hesperornis* is the most well-known hesperornithiform with the largest number of preserved skeletal remains and the widest North American geographical distribution, ranging from Arkansas to the Canadian Arctic (Figure 1) (Wilson et al., 2011; Wilson et al., 2016; Aotsuka and Sato, 2016; Bell and Chiappe, 2016). Most *Hesperornis* specimens are isolated elements from the hind limbs, pelvis, and vertebrae, but both partial and nearly complete skeletons are known (e.g., Carpenter, 2006; Aotsuka and Sato, 2016; Bell and Chiappe, 2016). WIS species ranged in size from *H. macdonaldi*, ~0.8 m long, to *H. gracilis*, *H. lumgairi*, and *H. regalis*, ≤ 1.9-2.0 m (length estimates based on Martin and Lim, 2002; Wilson et al., 2011; Aotsuka and Sato, 2016). The genus was largely marine to transitional-marine, but non-marine occurrences are known from the Campanian of Montana, Wyoming, and Alberta (Shufeldt, 1915; Fox, 1974; Case, 1987; DeMar and Breithaupt, 2008; Unpublished specimens: one UCMP specimen and nine YPM specimens [Supplement S1]) and the Maastrichtian of Montana (Tanaka et al., 2018; Supplement S1). Despite the abundance of *Hesperornis* and inferences made about their ecology, possible ecological relationships have not been quantified or predicted using distribution models. The purpose of this study is to determine the sedimentological, paleogeographical, and faunal community factors that most influence the WIS distribution of *Hesperornis* with emphasis on potential predator-prey and competitive relationships. A secondary objective is to test generalized linear modeling and occupancy modeling on extinct marine vertebrates and to apply novel techniques in marine vertebrate paleontology.

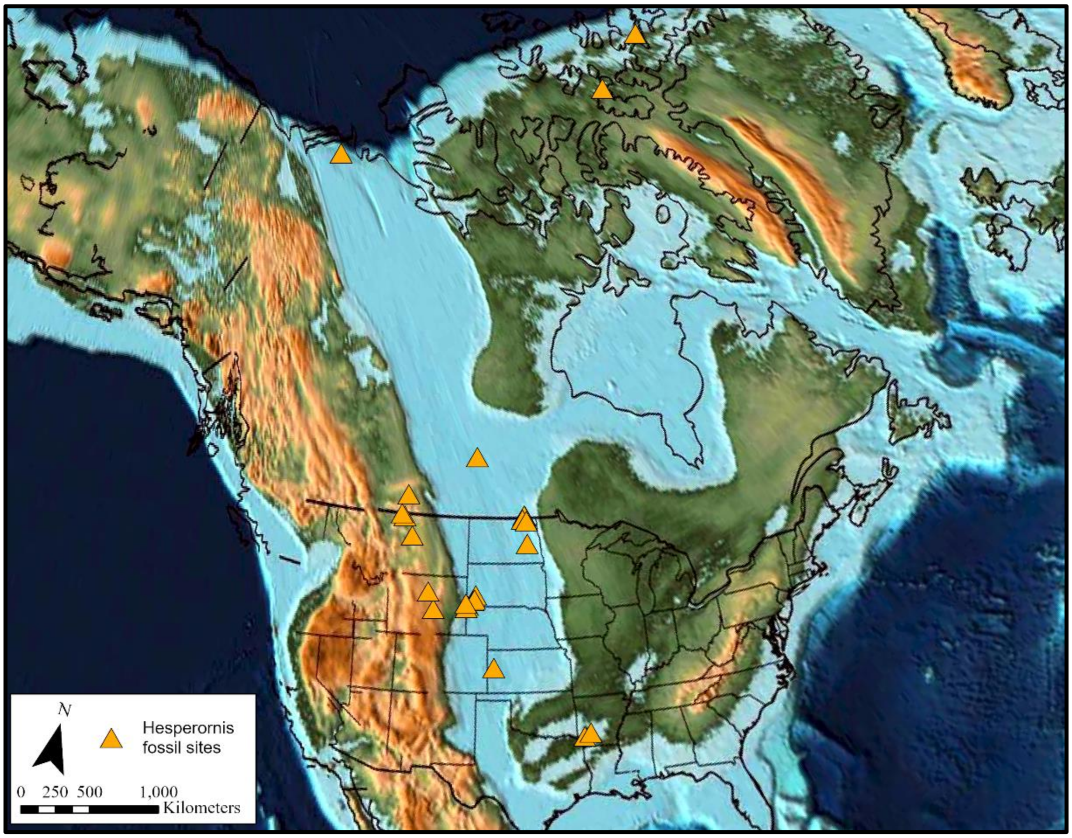

Figure 1. Campanian distribution of *Hesperornis* within the WIS and High Arctic. *Hesperornis*-bearing sites are reconstructed to the early middle Campanian (80 Ma) and depicted using an 80 Ma paleogeographic map (modified from Scotese, 2016). Symbols representing fossil localities are not to scale. Data were obtained from the Paleobiology Database, museum collections records, and published literature (see Supplement S2).

Almost all hesperornithiform dietary inferences are based on tooth and jaw morphology and mode of swimming (Elzanowski, 1983; Dumont et al., 2016; Wilson et al., 2016). While considered generalist feeders or pursuit divers of fish or squid (Elzanowski, 1983; Dumont et al., 2016; Wilson et al., 2016; Everhart, 2017), the only probable direct evidence of hesperornithiform diet are coprolites or a colonite associated with the *Fumicollis hoffmani* holotype from Kansas (UNSM 20030, formerly *Baptornis advenus*) (Martin and Tate, 1976; Bell and Chiappe, 2015). These trace fossils contain an *Enchodus* jaw and other fish bones, but the coprolite/colonite association with the skeleton remains tentative (Table 1) (Martin and Tate, 1976; Wilson et al., 2016; Everhart, 2017). While the fossil record has not yet revealed much direct evidence of the hesperornithiform diet, some fossils from South Dakota demonstrate interactions with predators and scavengers (Table 1). Based on known specimens, three taxa are identified as hesperornithiform predators or scavengers: polycotylid plesiosaurs, *Tylosaurus proriger*, and *Squalicorax* cf. *falcatus*.

Table 1. Hypothesized interspecific interactions between hesperornithiforms and other WIS taxa. The column "Ecological Role" refers to the hesperornithiform role in the interspecific interaction.

Ecological Role	**Age**	**Hesperornithiform Taxon**	**Other Taxa**	**References**
Predator	Late Coniacian to early Campanian	*Fumicollis hoffmani* (UNSM 20030; holotype; formerly *Baptornis advenus*)	*Enchodus* sp. and indeterminate fish (preserved in tentatively associated coprolites / colonites)	Martin and Tate (1976); Bell and Chiappe (2015)
Prey	Middle Campanian	*Hesperornis* sp. (YPM VPPU 17208.D)	Polycotylidae indet. (inferred from bite marks)	Martin et al. (2016)
	Early Campanian	*Hesperornis* sp. (SDSM 10439; Note: All five taxa have the same catalog number.)	*Tylosaurus proriger* Associated gut contents of *Tylosaurus* specimen: ?*Cretalamna* sp., *Clidastes* sp., and *Bananogmius* sp.	Martin and Bjork (1987); Martin et al. (2016)
	Middle to late Turonian	Hesperornithiformes indet. (SMM P2000.12.10)	*Squalicorax* cf. *falcatus* (may have scavenged the hesperornithiform; inferred from bite marks)	Hanks and Shimada (2002); Shimada and Hanks (2020)

Potential predator-prey relationships across geographic space are topics addressable by species distribution models (SDMs), a term used interchangeably with ecological niche models (ENMs). These models are a common form of distribution or niche modeling techniques applied in modern ecological and paleontological studies. SDMs rely on modeling algorithms to predict regional habitat suitability (i.e., the fit of environmental and ecosystem conditions), estimate the probability of presence, or predict and describe the factors that most influence the distribution of the target organism(s) (Elith and Leathwick, 2009; Elith et al., 2011; Robinson et al., 2011; Peterson et al., 2012; Elith and Franklin, 2013; Myers et al., 2015). Each model includes one or more environmental or biological variable(s) that could affect the pattern of species occurrence or abundance such as temperature, water depth, predation/competitive taxa, etc. These variables are termed covariates (meaning independent variables that may covary) or predictors.

Researchers have used SDMs for modern ecosystems and paleoenvironments to study niche stability, interspecific interactions, dispersal, conservation, invasive species proliferation, community dynamics, extinction event/biodiversity crisis survivorship, speciation and extinction rates, and climate change effects (e.g., Maguire and Stigall, 2008; Menke et al., 2009; Malizia and Stigall, 2011; Robinson et al., 2011; Svenning et al., 2011; Rovelli and Myers, 2016; Waterson et al., 2016; Carrier, 2018; MacKenzie et al., 2018). Non-marine SDM applications outnumber marine SDMs, with most modern analyses of marine ecosystems examining conservation planning, method evaluation, and theoretical ecology for fish and mammals compared to relatively few marine invertebrate studies (see Dambach and Rödder, 2011; Robinson et al., 2011; Melo-Merino et al., 2020, for reviews of modern marine research topics). Paleontological marine SDMs, while less abundant than non-marine applications, focus on invertebrates (e.g., Stigall Rode and Lieberman, 2005; Dudei and Stigall, 2010; Malizia and Stigall, 2011; Brame and Stigall, 2014; Pimiento et al., 2016; Rovelli and Myers, 2016; 2018; Carrier, 2018; Carotenuto et al., 2020). This leaves a gap in the application of SDMs to marine vertebrate paleoecosystems.

SDM species occurrence information includes four data types: presence-only, presence/background, presence/absence, and occupancy/detection data. The type of species occurrence information will determine which modeling algorithms should be used and the prediction generated using those algorithms. Presence-only models (*sensu stricto* Pearson, 2010; Guillera-Arroita et al., 2015), such as those created using BIOCLIM, use surveyed sites where the species was detected or found (species presences) to make inferences about the species distribution without environmental conditions from surrounding sites (Nix, 1986; Busby, 1991; Booth et al., 2014; Guillera-Arroita et al., 2015). Presence/background modeling algorithms (e.g., MaxEnt and GARP) focus on known species presences and incorporate these and background data to estimate relative habitat suitability (Stockwell and Peters, 1999; Phillips et al., 2004; 2006; Elith and Leathwick, 2009; Malizia and Stigall, 2011; Guillera-Arroita et al., 2015; Myers et al., 2015). Background data are randomly-chosen sites within the study area that characterize species distributions using the environmental conditions throughout the study area. These background points may exclude or include known species presences depending on the preference of the researcher and may be described as pseudo-absences (e.g., Elith and Leathwick, 2009; Pearson, 2010; Barbet-Massin et al., 2012).

In contrast to presence-only and presence/background methods, presence/absence models, such as generalized linear models (GLMs), include absence data recorded in field surveys (known absences) and environmental or biological conditions from all surveyed sites (e.g., Elith et al., 2006; Guillera-Arroita et al., 2015). Presence/absence models are advantageous because these models predict the probability of occupancy (i.e., probability of presence) rather than the relative habitat suitability predicted by presence/background models (e.g., Elith et al., 2011; Guillera-Arroita et al., 2015; Gelfand and Shirota, 2019). In other words, occupancy estimates the probability of presence for the target species rather than ranking sites by suitability. However, the estimation of occupancy or presence is biased due to imperfect detection; absences (or non-observations) may be either true absences or a failure to detect the target species (e.g., Elith and Franklin, 2013; Guillera-Arroita et al., 2015; MacKenzie et al., 2018). Imperfect detection is due to differences in an individual's surveying ability, differential outcrop preservation, or uneven collection practices.

Correction of biased occupancy requires a conceptual extension of GLMs known as occupancy modeling (alternatively, occupancy/detection or site-occupancy modeling) that uses occupancy/detection data. Both occupancy models and other presence/absence models estimate occupancy from presence/absence data, but occupancy models also estimate the probability of detection (p): the probability that the target species was observed if present at a site (i.e., the probability of observation) (MacKenzie et al., 2002; Elith and Franklin, 2013; Guillera-Arroita et al., 2015; Koshkina et al., 2017; MacKenzie et al., 2018). The detection probability for a site denotes the combined probability that a taxon was observed and the probability that it was truly present (i.e., was it living there and was it falsely detected?) (e.g., Guillera-Arroita et al., 2015; MacKenzie et al., 2018). For paleontological analyses, the detection probability can be considered both "preservation and discovery" (Liow, 2013:194). The detection probability differs from the occupancy probability with the latter denoting the probability of presence. The detection probability is estimated using the detection history, the collection of non-detections (p = 0) and detections (p = 1) recorded during repeated site sampling. Estimation of detection probabilities is most crucial when the target taxon is not observed (i.e., observed absence). Here, the detection probability allows a researcher to discriminate between true absences, where a taxon was not observed and does not inhabit a site, and false-negatives, where a taxon was not observed but was truly present (e.g., Lahoz-Monfort et al., 2014; Guillera-Arroita et al., 2015; MacKenzie et al., 2018).

The simultaneous estimation of detection and occupancy in occupancy modeling facilitates estimation of true occupancy (ψ), the probability of presence when imperfect detection is modeled. For clarity, the biased occupancy probability from most presence/absence models (including GLMs) is hereafter termed the probability of occurrence to distinguish it from the probability of true occupancy estimated by occupancy models. Despite biased occupancy estimates, GLMs and other presence/absence models have one advantage over occupancy models: GLMs can incorporate sites that are only sampled once and sites with multiple samples, leading to larger sample sizes than occupancy models which only use repeatedly sample sites.

Only six studies have used SDM to examine extinct nektonic marine species and two studies examined the past distribution of extant nektonic marine taxa (Bigg et al., 2008; Provan et al., 2009). Of these eight studies, only one investigated an extinct marine vertebrate (Pimiento et al., 2016). Rovelli and Myers (2016; 2018), Carrier (2018), Carrier and Myers (2018), and Carotenuto et al. (2020) incorporated ammonites and nautiloids which lived as nektonic to nektobenthic organisms. Pimiento et al. (2016) used fossil tooth occurrences of *Otodus* (= *Carcharocles*) *megalodon* (*sensu* Shimada et al., 2017) to examine possible extinction-causing factors. Bigg et al. (2008) and Provan et al. (2009) studied the distributions of the extant Atlantic cod (*Gadus morhua*) and the North Atlantic copepod (*Calanus finmarchicus*), respectively, during the Last Glacial Maximum. Paleontological SDM literature includes two occupancy model and two GLM applications. Liow (2013) used occupancy models to examine occupancy shifts for Late Ordovician brachiopods from the Cincinnatian Arch. Like most SDM studies regarding extinct marine organisms, that study did not include any nektonic organisms or vertebrates. Lawing et al. (2021) applied occupancy models to study the influence of detection variability on relative abundance of late Quaternary pollen taxa. The two GLM studies focused on non-marine taxa. Melchionna et al. (2018) used GLMs to investigate the extinction-causing triggers for Neanderthals (*Homo neanderthalensis*) during the Pleistocene. Eduardo et al. (2018) used GLMs to model South American mammal and caiman distributions during the late Pleistocene. Additional paleontological SDM applications are reviewed by Svenning et al. (2011) and Varela et al. (2011). It should be noted that Myers and Lieberman (2011) and Myers et al. (2013) investigated competition amongst predatory and durophagous marine vertebrates, and the relationship between mollusc geographic range size and survivorship, respectively, in the WIS. On the surface these studies may appear to represent SDMs (though the authors do not make this claim), but these studies cannot be considered SDMs because minimum bounding polygons were used to generate paleogeographic ranges from occurrences of included marine taxa rather than to relate the occurrences to paleoenvironmental or biological data.

This study represents the first GLM and occupancy modeling applications to characterize extinct marine vertebrate ecosystems and the first SDM analysis of *Hesperornis* occurrences. The methods used here incorporate absence data to enable estimation of occupancy rather than relative habitat suitability (Guillera-Arroita et al., 2015; MacKenzie et al., 2018). GLMs test larger samples of sites than occupancy models by including locality information from single-sample sites. Occupancy modeling, through collection of site detection histories, permits the identification of factors that may influence detectability of fossil taxa, such as differential collection and sampling methods or preservational biases (e.g., Liow, 2013; MacKenzie et al., 2018). The separation of these factors from covariates that influence occupancy should improve occupancy probability estimates and reduce false-absence frequency (e.g., Tyre et al., 2003; Dorazio, 2014; Lahoz-Monfort et al., 2014; Guillera-Arroita et al., 2015; MacKenzie et al., 2018). Comparison between GLMs and occupancy models identifies covariates or covariate groupings predicted by multiple model types to most influence *Hesperornis* occurrences. Each model type, while overlapping for 22 localities, contributes different information: single-sample sites from GLMs and detection histories from occupancy models.

Institutional abbreviations: **AMNH**: American Museum of Natural History, New York City, New York; **CFDC**: Canadian Fossil Discovery Center, Morden, Manitoba; **CMN**: Canadian Museum of Nature, Ottawa, Ontario; **FHSM**: Sternberg Museum of Natural History, Fort Hays State University, Hays, Kansas; **SDSM**: Museum of Geology, South

Dakota School of Mines and Technology, Rapid City, South Dakota; **SMU SMP**: Shuler Museum of Paleontology, Southern Methodist University, Dallas, Texas; **TMM**: Jackson School Museum of Earth History (formerly the Texas Memorial Museum), The University of Texas at Austin, Austin, Texas; **UCM**: University of Colorado Museum of Natural History, University of Colorado Boulder, Boulder, Colorado; **UCMP**: University of California Museum of Paleontology, Berkeley, California; **UNSM**: University of Nebraska State Museum, Lincoln, Nebraska; **YPM VPPU**: Yale Peabody Museum, Vertebrate Paleontology, Princeton University Collection, New Haven, Connecticut.

MATERIALS AND METHODS

Data Collection and Processing

Faunal occurrence and lithologic data were collected from the Paleobiology Database (PBDB), Integrated Digitized Biocollections database (iDigBio), museum collections records, and published literature using the search terms "*Hesperornis*," "Vertebrata," "Campanian," and a geopolitical region (i.e., state, province, or territory). These data represent Campanian fossil vertebrate-bearing localities across the WIS. Faunal occurrences from Texas were also obtained during collections visits to SMU SMP and the TMM. Collections visits to SDSM and FHSM provided additional faunal occurrences for South Dakota and Kansas, respectively. Site lithology and geochronologic age were determined using published literature.

Liow (2013:195) defined faunal sites as "a unique combination of a geographic location, a depositional sequence, and a facies for the single-time-interval occupancy model." This study follows a similar approach with lithology (mudrock, sandstone, or carbonate) used rather than facies. Faunal sites were grouped into a single locality if they fell within an approximately 10-km radius and were from the same formation or member. The 10-km buffer combines isolated faunal occurrences to reduce preservation and collection biases. While subjective, the 10-km buffer accounts in-part for the high mobility of WIS taxa that were likely a component of regional faunal assemblages. Localities were only recorded if they contained at least two taxa of genus or higher rank. Sites that lacked chronostratigraphic clarity (i.e., the source rock unit was unclear or spanned several geologic ages), had faunas generalized across many variable lithologies and depositional environments, or had an unknown georeferenced position were not included. These constraints resulted in a total of 61 fossil localities of which 26 bear *Hesperornis* material (Fig. 2). Some of the models used 22/61 Campanian fossil localities of which 11 bear *Hesperornis* material (Fig. 3). These models are described in the Data Analysis section below.

PBDB and iDigBio localities were checked against the referenced literature or museum collections to ensure accuracy. These localities were georeferenced using coordinates provided by the referenced article or through approximation in Google Earth Pro 7.3 (Google, LLC, 2020) using either a locality map or a site description. Localities listed in Public Land Survey System (PLSS) notation were placed in the center of the smallest known PLSS unit (unless the article noted otherwise) using Google Earth Pro. Localities recorded following the Dominion Land Survey (DLS) and the Alberta Township Survey System variant, the western Canada equivalents of the PLSS, were estimated using township and range grid shapefiles for Alberta and Saskatchewan in ArcMap 10.7.1 (ESRI, Inc., 2019). Geographic positions of sites follow decimal degree notation. It is noted in Supplement S2 if the online collections data aggregates did not properly place the specimens in geographic space.

If an updated taxonomic identification was found for sampled sites, the specimen identification was changed to follow the most recent article. Two examples are *Trinacromerum bonneri* and *Hainosaurus pembinensis* from the CFDC Manitoba Escarpment sites; these taxa were re-identified as *Dolichorhynchops* and *Tylosaurus* species, respectively (O’Keefe, 2008; Bullard and Caldwell, 2010). Reidentification of included specimens outside of literature revisions was beyond the scope of this project. Traditional terrestrial groups were ignored from sampled localities for analysis (although noted as present in Supplement S2). Excluded vertebrate taxa include all non-avian dinosaurs, non-mosasaurian squamates, Lissamphibia, and Mammalia. These taxa were either not present across most dataset localities or would not have lived within the same community. Non-tetrapod sarcopterygians were excluded because they are present at only three sites (low sample size): *Megalocoelacanthus dobiei* of Kansas (AMNH FF 20267 and the unpublished FHSM VP-18758) and *Coelacanthus granulatus* from Utah (UCM 95431) (Schwimmer et al., 1994; Dutel et al., 2012; Harrell and Ehret, 2019; Jacob Van Veldhuizen, pers. comm., 2020). Their limited geographical distribution within 1.5° of latitude also merits exclusion. Because this research is focused on vertebrate communities, invertebrate and plant taxa were also excluded.

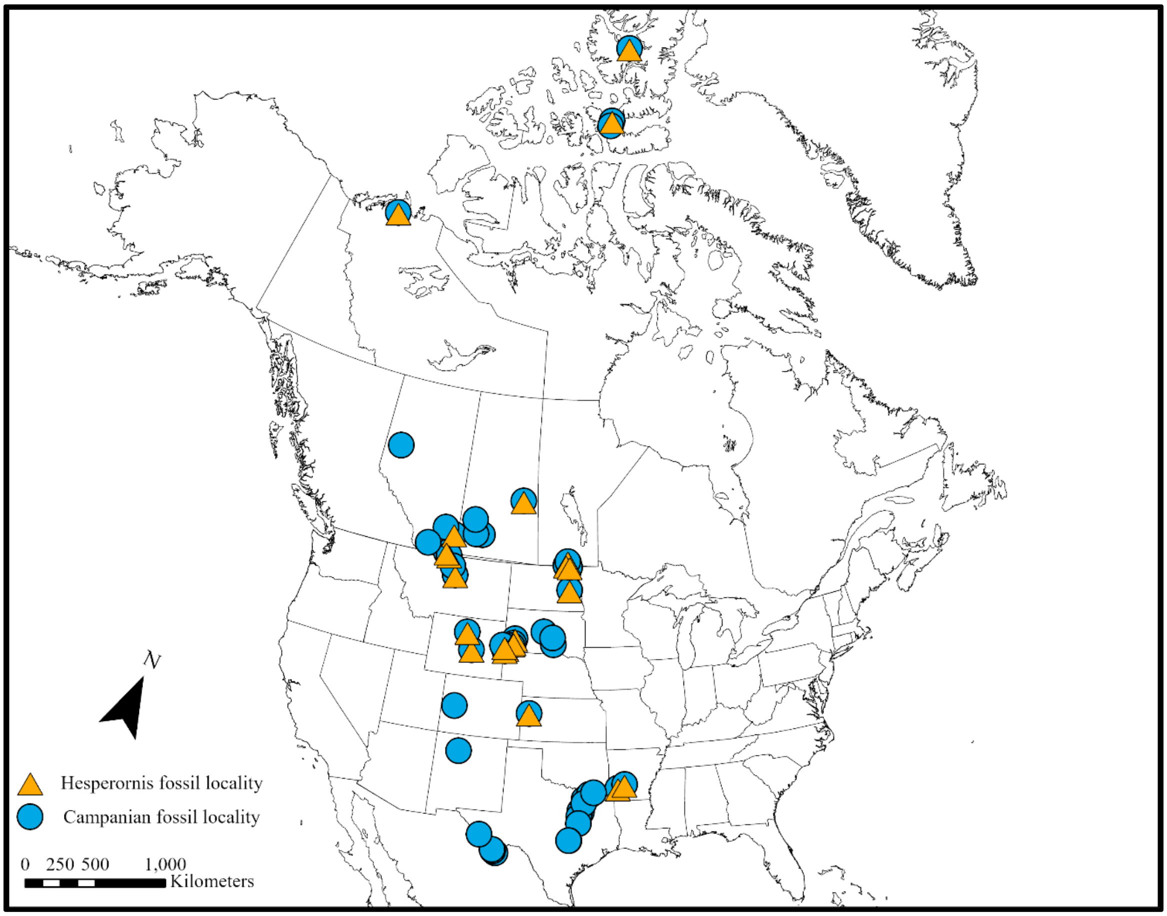

Figure 2. Map of Campanian fossil-bearing localities included in the full dataset GLMs. Orange triangles represent Campanian *Hesperornis* occurrences; blue circles represent Campanian fossil localities (inclusive of the *Hesperornis*-bearing sites). Symbols used to represent fossil localities are not to scale. Data were obtained from the Paleobiology Database, museum collections records, and published literature (see Supplements S2-S3).

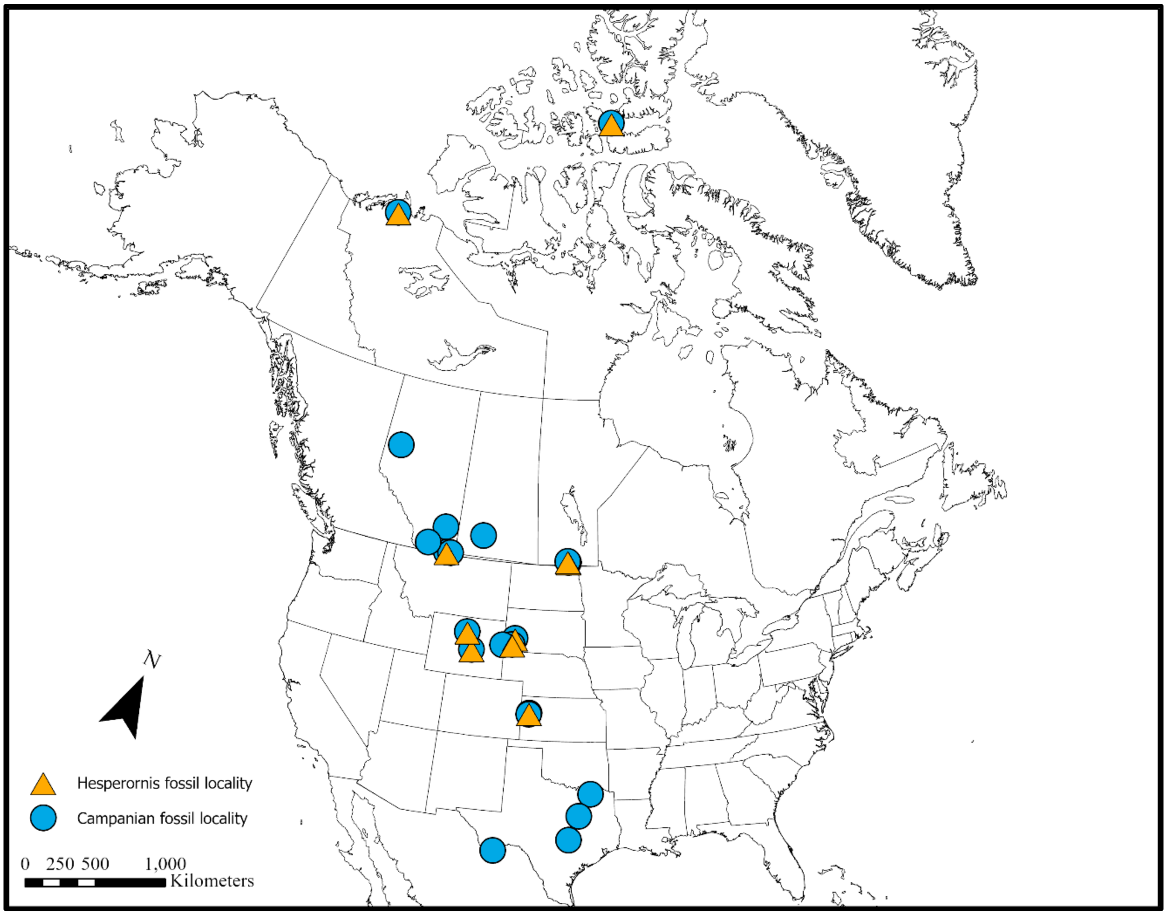

Figure 3. Map of Campanian fossil-bearing localities included in the reduced dataset GLMs and occupancy models. Orange triangles represent Campanian *Hesperornis* occurrences; blue circles represent Campanian fossil localities (inclusive of the *Hesperornis*-bearing sites). Symbols used to represent fossil localities are not to scale. Data were obtained from the Paleobiology Database, museum collections records, and published literature (see Supplements S2 and S4).

Thirty covariates were used for modeling the distribution of *Hesperornis*, the target species (Tables 2 and 3). Of these 30 variables, 24 covariates represent contemporaneous taxonomic occurrences and include both genera and larger clades

(Table 2). Of these covariates, *Tylosaurus*, Polycotylidae, *Squalicorax*, and *Enchodus* represent known or inferred ecological interactions with *Hesperornis* and other hesperornithiforms (Table 1). While interactions between *Enchodus* and *Fumicollis hoffmani* (UNSM 20030) or *Squalicorax* and an indeterminant hesperornithiform (SMM P2000.12.10) do not include *Hesperornis* (Martin and Tate, 1976; Bell et al., 2015; Shimada and Hanks, 2020), the similarly-sized *Hesperornis* might have had a similar ecological relationship with these organisms. Eight other genera were included because they occurred at six or more localities and were present in three or more faunal communities with *Hesperornis* (Table 2). Genera were examined rather than species to increase sample size and avoid taxonomic disputes (see Wilson et al., 2011; Aotsuka and Sato, 2016; Bell and Chiappe, 2016 for taxonomic discussions concerning *Hesperornis* spp.). Genera identified with a '?' or the comparative abbreviation 'cf.' were included to increase sample sizes and follow an occupancy modeling assumption that there are no incorrect identifications (i.e., false-positives) (MacKenzie et al., 2018). While false-positives can be modeled (e.g., Royle and Link, 2006; Chambert et al. 2015), it is beyond the scope of the current project. Eight larger taxonomic groups ('order' or 'class' rank in Linnean classification) and five smaller clades ('family,' 'parafamily,' or 'sub-family' rank, including Polycotylidae) were also examined (Table 2). The detection probabilities for each of the non-*Hesperornis* taxonomic occurrences are currently unknown as they were not the target species of this study.

Only a handful of paleo-SDMs incorporate biotic factors into their models. Most of the SDM/ENM papers by A. L. Stigall and co-authors examined Ordovician and Devonian benthic invertebrates with models incorporating biofacies (Stigall Rode and

Lieberman, 2005; Dudei and Stigall, 2010; Malizia and Stigall, 2011; Walls and Stigall, 2011; Brame and Stigall, 2014). These covariates include paleocommunities that represent invertebrate communities found in varying levels of water turbulence, different substrate types (i.e., deep/muddy to shallow/firm), anoxic conditions, continental settings, or dominance by one species (Stigall Rode and Lieberman, 2005; Dudei and Stigall, 2010; Malizia and Stigall, 2011; Walls and Stigall, 2011; Brame and Stigall, 2014). The influence of biofacies on the target species, however, was not interpreted despite being scored as a categorical or continuous variable. Maguire and Stigall (2009) use crocodilian presence/absence data as a proxy for paleotemperature in the Miocene-Pliocene Great Plains of North America. Crocodilian occurrences are used as further evidence for paleotemperature and vegetative shifts across the region that influenced species distributions within Equinae. Carotenuto et al. (2020) is the only paleo-SDM study to use occurrences of contemporaneous taxa as direct predictors (rather than a proxy) for the paleogeographic distribution of their target species. Both Maguire and Stigall (2009) and Carotenuto et al. (2020) interpolate occurrences of coeval species within their study area.

Three covariates describe general sedimentary lithologies: mudrock, sandstone, and carbonate (Table 3). The mudrock covariate contains shales, mudstones, and siltstones (i.e., fine-grained siliciclastics) while the carbonate covariate describes limestones, including chalks. Marls and calcareous mudstones/shales were split between the mudrock and carbonate covariates. The 24 taxa and three sedimentary lithologies were coded as binary values with 0 and 1 representing absence and presence, respectively.

Three spatial covariates were examined (Table 3): paleolatitude (°N) at 80 Ma, relative position in the WIS (WIS position), and outcrop area. Paleolatitude (a continuous variable) required conversion from modern latitude in GPlates 2.1.0 (Müller et al., 2018) using the Scotese (2016) paleogeographic reconstructions. For the GLMs, paleolatitudes were standardized between 0 and 1 by dividing the paleolatitudes by 90°N; 90°N represents the maximum latitude for the Northern Hemisphere. A different standardization method was used for the occupancy models because division of paleolatitude by 90°N tended to create model errors. Z-score transformation (e.g., Schumacker and Tomek, 2013) was used instead. This transformation subtracts the sample mean before dividing by the standard deviation of the sample. Resultant values follow the same statistical distribution shape (Warren et al., 2011) and maintain inter-value differences proportional to the original data (pers. obs.).

WIS position (a categorical variable) divides the WIS into thirds: west, middle, and east. This covariate was used instead of paleolongitude because the qualitative nature accounts for WIS shoreline curvature across paleolongitude lines. The WIS position covariate also roughly reflects bathymetry with the deepest water in the middle WIS (e.g., Longman et al., 1998; Lowery et al., 2018). Fossil localities were sorted into west, middle, and east categories by comparing modern positions to the Blakey (2014) and Scotese (2016) paleogeographic reconstructions. The Blakey (2014) reconstructions include the early-late Campanian WIS whereas the Scotese (2016) reconstructions only include the middle and late Campanian WIS. The rough groupings of sites into west, middle, and east should closely resemble quantified distances from either the western or eastern paleoshorelines. Quantified distances are less subjective when dividing sites into regions, but this quantitative covariate has not yet been tested. Paleolatitude and WIS position were used to examine potential habitat preferences of *Hesperornis* linked to geographic location in the WIS. These preferred regions or paleolatitudes may reflect sea surface temperature, bathymetry, or ecology.

Outcrop area (km^2) was approximated by clipping mapped geologic unit polygons to United States county boundaries and Canadian census division boundaries using ArcMap (sources included in Supplement S5). While not necessarily correlated with exposure area, outcrop area is a proxy for the relative amount of available rock and has been applied by multiple authors to address detection or sampling biases (e.g., Crampton et al., 2003; Uhen and Pyenson, 2007; Wall et al., 2009; Dunhill, 2011; 2012; Dunhill et al., 2012; Irmis et al., 2013). This covariate is used to assess if preservational bias influences *Hesperornis* occurrences and detection. The z-score transformation was used for outcrop area to reduce the magnitude difference between binary numbers (i.e., presences and absences) and tens to thousands of square kilometers.

Table 2. Taxonomic covariates used for modeling. Larger taxonomic groups denote clades that are designated as ‘order’ or ‘class’ rank in traditional Linnaean classification whereas taxonomic subgroups correspond to ‘family,’ ‘parafamily,’ or ‘sub-family’ rank.

Larger Taxonomic Group	**Taxonomic Subgroup**		**Genus**
Chondrichthyes			*Squalicorax* *
			Cretalamna
Actinopterygii			*Xiphactinus*
			Enchodus *
			Cimolichthys
Testudines			*Toxochelys*
Non-*Hesperornis* Aves			
Crocodyliformes			
Pterosauria			
Plesiosauria	Elasmosauridae		
	Polycotylidae *		*Dolichorhynchops*
Mosasauridae / Mosasauria	Russellosaurina		*Tylosaurus* *
		Plioplatecarpinae	*Platecarpus*
			Plioplatecarpus
	Mosasaurinae		*Clidastes* †

* Indicates a taxon hypothesized to have paleoecological interactions with *Hesperornis* or another hesperornithiform (see Table 1).

† Specimens included as *Clidastes* should be interpreted as non-monophyletic and likely a paraphyletic basal mosasaurine grade until the genus is better resolved, a problem that has been known for over 20 years (e.g., Bell, 1997; Christiansen and Bonde, 2002; Dutchak and Caldwell, 2009; Palci et al., 2013; Lively, 2018; Madzia and Cau, 2020).

Table 3. Non-taxonomic covariates used for modeling.

Sedimentary Lithology	**Spatial Covariate**	
	Covariate Name	**Transformation for Analysis**
Mudrock	Paleolatitude (°N) * - Standardized at 80 Ma -	Divided by 90°N (GLMs) Z-score transformed (occupancy models)
Sandstone	WIS position	None
Carbonate	Outcrop area (km^2)	Z-score transformed

* Paleolatitude is hypothesized to influence the distribution of *Hesperornis* by Nicholls and Russell (1990), Feduccia (1999), and Rees and Lindgren (2005).

Maps depicting *Hesperornis*-bearing localities and other sampled sites were created in ArcMap 10.7.1 and ArcGIS Pro 2.8.0 (ESRI, 2021). Site data and maps of North America were formatted for the North American Datum 1983 and projected to North America Lambert Conformal Conic. For Figure 1, modern geographic coordinates of Campanian *Hesperornis* localities were converted to a paleogeographic location (both in decimal degrees) using the Scotese (2016) paleogeographic reconstructions and GPlates to create a locality shapefile. This geographic conversion was used to account for tectonic movement of the North American Plate that included translation and rotation of localities. All localities were reconstructed for the early middle Campanian (80 Ma) which is more site representative of the dataset (early-late Campanian) than the late Campanian (75 Ma) reconstruction (Scotese, 2016) (Fig. 1). Figures 2 and 3 were created using political boundary shapefiles derived from ArcGIS Online (ESRI, Inc., 2020). The modern coordinates for Campanian fossil localities and *Hesperornis*-bearing sites were used.

The supplemental materials contain data on fossil assemblages and localities (Supplements S2-S4). Sources of faunal assemblages and map data are also provided (Supplement S5).

Data Analysis

All results except for occupancy models were produced in the software and programing language R 4.0.4 (R Core Team, 2021). R codes and formatted data used for analyses are in Supplements S3, S4, and S6. Prior to running the GLMs and occupancy models, the 24 taxonomic covariates (Table 2) were compared to each other, not *Hesperornis*, to assess independence using Jaccard's similarity index (Boyle et al., 1990; Real and Vargas, 1996). This was accomplished using the R packages 'vegan' and 'ade4' (Chessel et al., 2004; Dray and Dufour, 2007; Dray et al., 2007; Oksanen et al., 2019). Though typically applied to investigate community similarity between two sites using presence and absence data, Jaccard's index was used to compare pairwise occurrences of the 24 taxonomic covariates and their degree of similarity. This index was chosen over other similarity indices because it does not depend on shared site absences or the total sample size (Boyle et al., 1990; Real and Vargas, 1996; Robert Channell, pers. comm., 2020). Similarity values ≥ 80% among taxa or communities are generally considered noteworthy (Robert Channell, pers. comm., 2020) and this threshold is followed here. Pairings between a taxonomic covariate and itself or with its more inclusive taxonomic group (e.g., *Xiphactinus* and Actinopterygii) lacked independence and were ignored. Predicted values range between 0 and 1 with 0 representing a pairwise relationship where the occurrences are most dissimilar and 1 representing full similarity. High similarity values indicate two taxa whose co-occurrences likely reflect an ecological relationship or both taxa shared environmental preferences. If two taxa had similar occurrences (similarity values ≥ 80%), this would indicate nonindependence between the two covariates and only one taxon of the pair could provide strong insight into the distribution of *Hesperornis*. The occurrences of the second taxon would provide no additional information and this taxonomic covariate would be removed before to running the SDMs.

Generalized Linear Modeling

Generalized linear models (GLMs) are modified linear regression models that can incorporate data that violate normal distribution assumptions common to ecological data (Guisan et al., 2002; Agresti, 2013). These models have two components: maximum likelihood estimation and a link function (Guisan et al., 2002; Elith et al., 2006). Likelihood is the probability, multiplied by a constant, that a hypothesis explains the observed data and maximum likelihood estimation is the method that identifies the combination of covariate estimates that produce the largest value from a likelihood function (Hastie et al., 2009; James et al., 2013; Etz, 2018; MacKenzie et al., 2018). A hypothesis with a higher likelihood has more support given the data than a hypothesis with a smaller likelihood (Etz, 2018). The second GLM component, the link function, expresses covariate estimates as a linear equation to explain the response variable (Guisan et al., 2002; Hastie et al., 2009; MacKenzie et al., 2018). In this study, *Hesperornis* occurrences are the response variable

Two sets of GLMs were generated in R for this study. One GLM set was created using a modified R script originally written by Dr. Robert Channell of Fort Hays State University. This set incorporated the full dataset (61 localities) (Fig. 2). The second set used a reduced dataset of 22 localities and is comparable to the occupancy models (see below) (Fig. 3). Unfortunately, outcrop area tended to create fitting errors in both GLM sets, likely caused by a difference in magnitude between outcrop area and binary covariates. Removal of this covariate reduced the number of models afflicted by errors and resulted in only 29 covariates used for most GLM analyses. Outcrop area, however, did not produce errors in the occupancy models.

The R script requires the packages 'ResourceSelection,' 'boot,' and 'jtools' (Davison and Hinkley, 1997; Lele et al., 2019; Canty and Ripley, 2020; Long, 2020). After loading the full dataset and specifying the model covariates, the variables were scaled with a z-score standardization (Schumacker and Tomek, 2013) and incorporated into the model dataframe (i.e., the data table or array). The dataframe was then split into *Hesperornis* presences and absences. Jackknife resampling (e.g., Schumacker and Tomek, 2013) was completed for 1000 randomizations to subsample 26 of the 35 absences from the dataset. This subsampling created a balanced GLM (i.e., equal presences and absences) to reduce statistical error that could be generated from unequal presences and absences. Once subsampling was complete, the absences were recombined with the presences to form a single balanced GLM dataframe. The GLM was then built using a logistic link (logit) function that transforms covariate values into probabilities to follow a linear model (e.g., Burnham and Anderson, 2002; Agresti, 2013; James et al., 2013; MacKenzie et al., 2018). This GLM was fit to the dataframe. Overall GLM significance was assessed using the R function anova() to compare the GLMs with covariates to the null model that lacked covariates.

GLM performance was assessed using Akaike's Information theoretic Criterion (AIC) to describe the relative information loss when the model is retained (Akaike, 1973; 1974; MacKenzie et al., 2018). AIC can be calculated using the following equation:

$$AIC = -2\,ln(L(\hat{\theta}|x)) + 2\delta \qquad \text{(Eq. 1)}$$

Where $ln(L(\hat{\theta}|x))$ represents the likelihood function and δ indicates the number of modeled variables (Akaike, 1973; 1974; MacKenzie et al., 2018). The first term, , describes the unexplained model variation and the second, , is a penalty term that prevents model improvement every time a new covariate is added. The second term encourages parsimony in model selection. Models with a lower AIC value retain the most information and are "estimated to be 'closest' to the unknown reality that generated the data" (Burnham and Anderson, 2002:62; MacKenzie et al., 2018). The differences in AIC values (ΔAIC or Δ_i) are examined to rank models by the amount of information lost with lower AIC values being better (Burnham and Anderson, 2002; Burnham et al., 2011; MacKenzie et al., 2018). ΔAIC is determined by the following equation:

$$\Delta AIC_k = AIC_k - AIC_{min} \qquad \text{(Eq. 2)}$$

where *k* indicates the model rank and *min* identifies the model with the lowest AIC value (Burnham and Anderson, 2002; Burnham et al., 2011; MacKenzie et al., 2018). Models with small ΔAIC compared to the model with the smallest AIC are most supported as explanative of the data. The relative proportion of model support is based on an evidence ratio, that is, the probability or likelihood ratio between the highest-ranked model and any other model (Burnham et al., 2011). The evidence ratio enables ΔAIC values to be described by relative likelihood values representing the amount of model support. ΔAIC ≤ 2 is a common threshold for the most supported models (Burnham and Anderson, 2002; Burnham et al., 2011; MacKenzie et al., 2018). With ΔAIC = 2, a model is approximately 2.7 times less likely than the highest-ranked model (Burnham et al., 2011, Table 1). In this study, the highest-ranked models are those with ΔAIC ≤ 2, following Burnham and Anderson (2002), and are used for ecological interpretations.

GLM data were assumed to be derived from a binomial distribution because occurrence has two states: present (1) and absent (0). GLM analysis in R returns p-values and estimates for each covariate coefficient and the intercept. Each coefficient has a sign (positive or negative) that indicates the effect (increase or decrease, respectively) the covariate exerts on *Hesperornis* occupancy. The intercept identifies the occurrence probability when the model covariates equal 0 or are not present at a site. R also calculates an AIC value and null and residual deviances for each model. Null and residual deviances were used to calculate the explained deviance or the explained data variation in *Hesperornis* occurrences. Explained deviance is a 'pseudo-R^2' value derived from the following equation (modified from McFadden, 1974:Eq. 30; Dobson and Barnett, 2008:137):

$$Explained\ deviance = \frac{Null\ deviance - Residual\ deviance}{Null\ deviance} = 1 - \frac{Residual\ deviance}{Null\ deviance} \qquad \text{(Eq. 3)}$$

The second GLM set includes a reduced dataset of 22 Campanian fossil-bearing localities with 11 preserving *Hesperornis* (Fig. 3). These are the same localities that contain two or more sites in the occupancy models (see below) for a more direct comparison. The modified R script was not necessary for the reduced dataset GLMs because the count of presences and absences is equal. Instead, the standard GLM function in R, glm() was used. GLMs were considered a good fit for the data if the models were significantly different from the null model (i.e., a model with no covariates).

Occupancy Modeling

Single-season occupancy models were created and run in PRESENCE v. 2.13.16 (Hines, 2006), an occupancy modeling program that estimates the occupancy and detection probabilities simultaneously. These models, which use maximum likelihood estimation and link functions (e.g., MacKenzie et al., 2018), can be constructed for one taxon (single-species model) or multiple taxa (multi-species model) and for one or more seasons. A season is one surveying period of sampled sites. For this study, only single-season models were used representing the entire Campanian; subdividing the Campanian into early, middle, and late would split the sample size of the current dataset and likely reduce result reliability.

Occupancy modeling necessitates multiple visits to a site for taxonomic sampling to build the detection history. Consequently, the dataset used in PRESENCE was restricted to 22 localities that combined two or more sites within a 10-km buffer to estimate occupancy and detection probabilities (Supplement S4). Of these 22 localities, *Hesperornis* was present in half (Fig. 3). *Hesperornis* occurrence data were entered into the Data Input Form in PRESENCE. The 30 covariates (Tables 2 and 3) were imported into the Site Covars tab of the Data Input Form. All PRESENCE analyses were run as simple single-season models using 1000 bootstraps, 31 surveys (the maximum number of sites combined into one sampled locality), and one observation method (fossil occurrence data collection from previously identified specimens) within the season. No sampling occasion covariates were used because, with the lack of additional information, the localities were assumed to have been collected and studied in a similar manner.

Initially, models were run with a single covariate for either the occupancy or detection probability of *Hesperornis*, while the other probability was held constant. This established a covariate baseline. The 24 taxonomic covariates, paleolatitude, and WIS position were used for the occupancy probability, while outcrop area was used only in the detection probability. Outcrop area is controlled by erosional and depositional rates and this covariate would not have impacted *Hesperornis* occurrences in life. The lithological covariates were used for either probability but not both simultaneously. Each lithology reflects depositional environments that may be preferred by *Hesperornis* or more conducive to preservation of *Hesperornis* fossils. All single-covariate models were compared with the null occupancy model, $\psi(.),p(.)$, where ψ and p are held constant for all sites, to evaluate if covariates affect predicted values of ψ and p. In the null occupancy model, ψ equals the proportion of known *Hesperornis* presences over the total sites (0.500 in this study) and $p = 1$ (perfect detection). PRESENCE automatically calculates the covariate coefficients and the probabilities of occupancy and detection for each site and model. As with the GLMs, the covariate coefficient sign denotes the effect on the *Hesperornis* distribution. Occupancy model performance was assessed by AIC. Model and covariate statistical significance were not assessed in the occupancy models because p-values were not estimated, as likelihood estimation is the focus of these models.

The covariates from GLMs and occupancy models that performed better than the null model (i.e., returned a lower AIC value) were run again in various combinations until new models failed to fall below the AIC value of the highest-ranked model. This method was used to determine which covariate combinations (hypotheses) most explain the data because automatic testing of covariate combinations via automated step-wise regression methods are limited. These functions only evaluate a few models, introduce parameter estimation bias, tend to include covariates that are irrelevant to the target species, suggest overconfidence in the highest-ranked model, and do not present models that are ranked below the highest-ranked model (Babyak et al., 2004; Whittingham et al., 2006; Burnham et al., 2011). Covariates with AIC values below the null reduced the performance of models even when the low AIC covariates were paired with higher AIC covariates above the null model.

Occupancy model fit was assessed using Pearson's chi-square test to compare the observed χ^2 value from the raw dataset to the average χ^2 generated by conducting a parametric bootstrap of the dataset (Burnham and Anderson, 2002; MacKenzie et al., 2018). If the observed χ^2 value is significantly larger than the bootstrapped χ^2 value, then the model is considered as a poor fit for the data. Prior to assessing each model, however, the 'global'/most general model, the model that incorporates the most covariates, must be assessed for model fit using Pearson's chi-square test and parametric bootstrapping. Fit of this model to the data is considered indicative that more parsimonious models can also fit the data (Burnham and Anderson, 2002; MacKenzie et al., 2018).

Non-SDM Tests

Separate tests were conducted in R to determine if outcrop area (km^2), modern latitude (°N), paleolatitude (°N), and WIS position significantly influence the number of *Hesperornis* specimens (p-value < 0.0125 using the Bonferroni Correction) (e.g., Armstrong, 2014). These tests use *Hesperornis* specimen counts rather than occurrence data to provide additional insight into preservational biases against *Hesperornis* and/or *Hesperornis* habitat preferences. Spearman's rank correlation was used to evaluate raw outcrop area, modern latitude, paleolatitude, and region of the WIS because the occurrence data did not meet the assumptions required by linear regression or Pearson's product moment correlation (Schumacker and Tomek, 2013; Heumann and Shalabh, 2016). Specifically, the data failed to meet normality and homoscedasticity (equal variance) assumptions. R returned the Spearman correlation coefficient (ρ) and a p-value. ρ ranges from -1 to +1 with positive and negative values indicating positive or negative linear rank associations, respectively (e.g., Artusi et al., 2002). Spearman's rank correlation would indicate the strength and direction (positive or negative) of the association between latitudinal/paleolatitudinal position, WIS region, or outcrop area and the number of *Hesperornis* specimens. Plots of the data may also demonstrate heavily sampled latitudes, paleolatitudes preferred by *Hesperornis*, or regions of the WIS and preservational biases toward certain outcrop area sizes.

A Kruskal-Wallis test was used to examine potential geographic bias of fossil localities using three samples (west, middle, and east). An analysis of variance (ANOVA) could not be used because the *Hesperornis* occurrence data failed to meet the normality assumption (Dalgaard, 2008). The Kruskal-Wallis test evaluates the differences in sample population medians (Dalgaard, 2008). In this study, a significant difference ($p < 0.0125$) in the number of *Hesperornis* specimens between WIS regions could indicate a preservational bias or habitat preference toward one or more regions.

RESULTS

Jaccard's index of similarity results find that the occurrences of non-*Hesperornis* avians or Crocodyliformes with *Plioplatecarpus* are the most dissimilar (0%). Plesiosauria and *Enchodus* are the most similar at 60% of sites. The relatively low similarity scores (< 80%) returned in the Jaccard's index analysis in general supports independence among the 24 taxonomic covariates. Full results of the Jaccard's index analysis, highest-ranked GLMs, highest-ranked occupancy models, and non-SDM tests for preservational bias or habitat preference are presented in Supplements S7-S12.

Results of Generalized Linear Model Analyses

Eighty-three GLMs were generated with the full dataset. Eight of these models were excluded because they returned errors when fit to the data. Of the remaining 75 models, all but five have AIC values that are smaller than the null model (AIC = 85.23; ΔAIC = 32.73). Only the two highest-ranked models (ΔAIC ≤ 2) are presented in Table 4 with the rest included in Supplement S9. All two highest-ranked models are statistically significant (p-value < 0.001) and contain the covariates Elasmosauridae, *Toxochelys*, and paleolatitude. The highest-ranked GLM (AIC = 52.503) contains four covariates: Elasmosauridae, Actinopterygii, *Toxochelys*, and paleolatitude. The model has a total explained deviance/variation of 62.2%. The second highest-ranked model (ΔAIC = 0.740) is similarly constructed with the exception of Actinopterygii. Nearly all covariates in the two highest-ranked models were significant (p-value < 0.05) with only Actinopterygii recovered as non-significant in Model 2 (p-value = 0.121). Coefficient estimates for all two highest-ranked models were positive except for Elasmosauridae (Supplements S7 and S10).

The reduced GLM dataset was used to create 115 GLMs. Of these, 30 had to be excluded due to fitting or convergence errors. Of the 85 included models, 30 models return higher AIC values than the null model (AIC = 32.498; ΔAIC = 17.250). The 15 highest-ranked reduced dataset GLMs (ΔAIC ≤ 2) are listed in Table 5. The results of the remaining models are included in Supplements S7 and S11. The reduced dataset GLM with the lowest AIC includes the covariates of Actinopterygii, non-*Hesperornis* Aves, Elasmosauridae, and paleolatitude (AIC = 15.248; ΔAIC = 0.000; p-value < 0.001; explained deviance = 0.828). While the overall model is significant, no covariates in the model show significance, though Elasmosauridae (p-value = 0.088) and paleolatitude (p-value = 0.078) were marginally significant. Of the 12 covariates present in the 15 highest-ranked models, only paleolatitude (p-values < 0.048) and Elasmosauridae (p-value = 0.039) have statistically significant p-values for 3/15 and 1/15 highest-ranked models, respectively (Supplements S7 and S10). No other covariates show statistical significance in the highest-ranked models. Elasmosauridae, *Plioplatecarpus*, carbonate (except for one model), and mudrock have a negative impact on *Hesperornis* occurrences based on the covariate coefficient signs. The other covariates are positive. All 15 models with ΔAIC ≤ 2 are statistically significant (p-value < 0.001). The 15 highest-ranked reduced dataset GLMs are characterized by three repeating groupings of covariates that include some model overlap. The most common grouping appeared seven times: Elasmosauridae + *Squalicorax* + paleolatitude. Elasmosauridae + non-*Hesperornis* Aves + paleolatitude appeared five times while Elasmosauridae + Testudines + paleolatitude appeared three times.

The reduced dataset GLMs seem to be the least reliable of the three model types. This model type did not produce a general covariate grouping for the highest-ranked models like the other two model types. Instead, nine covariate groupings were identified that differed by one covariate. In addition, most covariates in the highest-ranked reduced dataset GLMs were not statistically significant. This contrasts with the highest-ranked full dataset GLMs that have nearly all significant covariates and is likely related to the small sample size of the reduced dataset GLMs. Only Elasmosauridae and paleolatitude were occasionally significant in the reduced dataset GLMs for 1/15 and 3/15 models, respectively. Lastly, the reduced dataset GLMs also returned more fitting errors (30 total) resulting in more excluded models than the other two model types. This count of excluded models is nearly four times higher than the full dataset GLMs (8 excluded) and one and one-half as many exclusions as the occupancy models (21 excluded) (Supplements S7, S9, S11, and S12). The combination of a smaller sample size (22 localities) and the inability to estimate detection probabilities likely reduced the reliability of reduced dataset GLM results and their ability to determine covariate significance. The reduced dataset GLMs will not be discussed in-depth further.

Table 4. Full dataset GLM results for $\Delta\text{AIC} \leq 2$. Explained deviances were calculated using Eq. 3. ‘Std’ is an abbreviation for the use standardization techniques described in the Materials and Methods. Significant covariates and p-values are highlighted in red. The p-value column represents the significance of the overall model. Null and residual deviances for these models are presented in Supplements S7 and S9.

Model Rank	**Model**	**AIC (ΔAIC)**	**Explained Deviance**	**Overall Significance (p-value)**
1	Elasmosauridae, Actinopterygii, *Toxochelys*, and StdPaleolatitude	52.503 (0.000)	0.622	< 0.001
2	Elasmosauridae, *Toxochelys*, and StdPaleolatitude	53.243 (0.740)	0.601	< 0.001
	Threshold for Highest-Ranked Models	(2)		
Null	None	85.230 (32.727)	0.000	Not applicable

Table 5. Reduced dataset GLM results for ΔAIC ≤ 2. Significant covariates and p-values (< 0.05) are highlighted in red. Other values are presented in Supplements S7 and S11.

Model Rank	**Model**	**AIC (ΔAIC)**	**Explained Deviance**	**Overall Significance (p-value)**
1	Elasmosauridae, Actinopterygii, Non-*Hesperornis* Aves, and StdPaleolatitude	15.248 (0.000)	0.828	< 0.001
2	Elasmosauridae, Non-*Hesperornis* Aves, and StdPaleolatitude	15.419 (0.171)	0.757	< 0.001
3	Elasmosauridae, Actinopterygii, *Squalicorax*, and StdPaleolatitude	15.436 (0.188)	0.822	< 0.001
4	Elasmosauridae, Testudines, Non-*Hesperornis* Aves, and StdPaleolatitude	15.611 (0.363)	0.816	< 0.001
5	Elasmosauridae, *Squalicorax*, and StdPaleolatitude	15.765 (0.517)	0.745	< 0.001
6	Elasmosauridae, Chondrichthyes, Non-*Hesperornis* Aves, and StdPaleolatitude	15.900 (0.652)	0.807	< 0.001
7	Elasmosauridae, Testudines, *Squalicorax*, and StdPaleolatitude	15.940 (0.692)	0.805	< 0.001
8	Elasmosauridae, Crocodyliformes, and StdPaleolatitude	16.201 (0.953)	0.731	< 0.001
9	Elasmosauridae, *Squalicorax*, *Enchodus*, and StdPaleolatitude	16.213 (0.965)	0.796	< 0.001
10	Elasmosauridae, Non-*Hesperornis* Aves, Pterosauria, and StdPaleolatitude	16.419 (1.171)	0.790	< 0.001
11	Elasmosauridae, Mosasaurinae, *Squalicorax*, and StdPaleolatitude	16.439 (1.191)	0.789	< 0.001
12	Elasmosauridae, Testudines, and StdPaleolatitude	16.685 (1.437)	0.715	< 0.001
13	Elasmosauridae, Mosasaurinae, *Squalicorax*, and StdPaleolatitude	16.826 (1.578)	0.711	< 0.001
14	Pterosauria, Elasmosauridae, *Squalicorax*, and StdPaleolatitude	16.984 (1.736)	0.771	< 0.001
15	Elasmosauridae, Plioplatecarpinae, *Squalicorax*, and StdPaleolatitude	17.187 (1.939)	0.764	< 0.001
	Threshold for Highest-Ranked Models	(2)		
Null	None	32.498 (17.250)	0.000	N/A

Results of the Occupancy Model Analyses

One hundred and eighteen models were generated in PRESENCE (Supplements S7 and S12). Twenty-one of these models were excluded due to potential convergence errors or negative values in the variance-covariance matrix included in the PRESENCE output. Only five of the remaining 97 models have ΔAIC ≤ 2 (Table 6) and 12 models had larger AIC values than the null model (Supplement S12). The highest-ranked model (AIC = 148.625) includes Elasmosauridae, paleolatitude, and position in the WIS as covariates that influenced ψ while carbonate and outcrop area influence the detection probability (p). The remaining four models differ from the highest-ranked model by the addition of an extra taxon, *Squalicorax*, *Tylosaurus*, or *Platecarpus*, or the subtraction of outcrop area as a detection covariate. Covariate coefficient signs (+ or -) are constant across all four highest-ranked models with positive signs returned for paleolatitude, position in the WIS, *Squalicorax*, and *Tylosaurus* (Supplement S10). Negative signs were returned for Elasmosauridae, carbonate, and outcrop area. The other 90 occupancy models are presented in Supplement S12.

Table 6. Occupancy model results for ΔAIC ≤ 2. Symbols: ψ: probability of occupancy; p: probability of detection; (.): period notation, which indicates that the probability was held constant. Additional model information is included in Supplements S7 and S12.

Model Rank	**Model**	**AIC (ΔAIC)**	**Model Likelihood**	**-2*Log Likelihood**
1	ψ(Elasmosauridae, StdPaleolatitude, WIS Position), p(Carbonate, StdOutcrop Area)	148.625 (0.000)	1.000	138.625
2	ψ(Elasmosauridae, *Squalicorax*, StdPaleolatitude, WIS Position), p(Carbonate, StdOutcrop Area)	148.694 (0.069)	0.970	136.694
3	ψ(Elasmosauridae, *Tylosaurus*, StdPaleolatitude, WIS Position), p(Carbonate, StdOutcrop Area)	149.165 (0.540)	0.763	137.165
4	ψ(Elasmosauridae, StdPaleolatitude, WIS position), p(Carbonate)	149.995 (1.370)	0.1369	141.995
5	ψ(Elasmosauridae, *Platecarpus*, StdPaleolatitude, WIS Position), p(Carbonate, StdOutcrop Area)	150.299 (1.674)	0.434	138.299
	Threshold for Highest-Ranked Models	(2)		
Null	ψ(.), p(.)	186.287 (37.662)	0.000	182.287

Model Comparisons

A comparison between the full dataset GLMs and occupancy models is presented in Table 7 using highest-ranked models (ΔAIC ≤ 2). The full dataset GLMs have an overall covariate grouping of Elasmosauridae + *Toxochelys* + paleolatitude. The covariate grouping of Elasmosauridae + carbonate + paleolatitude + WIS position + outcrop area defines most of the occupancy models. The highest-ranked full dataset GLMs and occupancy models share one model grouping: Elasmosauridae + paleolatitude.

Table 7. Covariate groupings shared among the highest-ranked models (ΔAIC ≤ 2).

	Covariates
Full Dataset GLMs (2 models)	Elasmosauridae *Toxochelys* Paleolatitude
Occupancy Models (5 models)	Elasmosauridae Paleolatitude Position in the WIS Carbonate * Outcrop area * Note: These covariates are in all five models except for outcrop area (4/5 models).
All Model Types (7 models)	Elasmosauridae Paleolatitude

* Covariate was modeled as a factor of the detection probability.

Results of Non-SDM Tests

The Spearman's rank correlation test for outcrop area finds no significant linear association between the number of *Hesperornis* specimens and outcrop area (ρ = 0.005, S = 2909.5, p-value = 0.980) (Table 8; Fig. 4). There are three outliers that are qualitatively located well outside of the main cluster of plotted points (the red circles in Fig. 4A). These sites correspond to the Pembina Member of the Manitoba Escarpment where 99 CFDC specimens of *Hesperornis* were recorded, the expansive Smoking Hills Formation deposits along the Anderson River, Northwest Territories, and the Pierre Shale deposits of east-central Saskatchewan. Removal of these outliers also results in a non-significant correlation (ρ = -0.135, S = 2297.2, p-value = 0.539).

A comparison between the number of *Hesperornis* specimens and latitude using Spearman's rank correlation test finds a non-significant linear relationship (ρ = 0.147, S =

2493.8, p-value = 0.472) (Table 8; Fig. 5A). Four outliers are present and represent the CFDC Pembina Member-bearing sites of the Manitoba Escarpment (49.3°N) and three Arctic localities (> 66.5°N). If the four outlying points are removed, the association becomes stronger but remains non-significant ($\rho = 0.208$, S = 1402.8, p-value = 0.353) and the data remain scattered (Fig. 5B). Spearman's correlation tests for paleolatitude and the number of *Hesperornis* specimens returned similar non-significant correlations with outliers ($\rho = 0.043$, S = 2799.8, p-value = 0.836) and without outliers ($\rho = 0.077$, S = 1634, p-value = 0.732) (Table 8; Figs. 5C-D). The lack of non-significant linear correlation between paleolatitude and the number of *Hesperornis* specimens is at odds with the results of the SDMs which predict paleolatitude as a major influence on *Hesperornis* occurrences. Figures 5C and 5D, however, indicate a possible non-linear association between *Hesperornis* specimen counts and paleolatitude with most *Hesperornis* specimens concentrated at mid-latitudes (~49-58°N). Aggregations at these paleolatitudes may help explain the ecological role of latitude on *Hesperornis* as detected by the SDMs (see Discussion).

The Kruskal-Wallis rank sum test for position in the WIS finds no significant difference in median *Hesperornis* specimen counts among regions ($\chi^2 = 1.751$, df = 2, p-value = 0.417) (Fig. 6). Spearman's rank correlation test did not find a significant linear correlation between position in the WIS and the number of *Hesperornis* specimens ($\rho = 0.094$, S = 2650.5, p-value = 0.648) (Table 8; Fig. 7). Plots of the data show an outlier present in the sample of points from the eastern region of the WIS that represents the CFDC Pembina Member-bearing sites of the Manitoba Escarpment (Figs. 6A and 7A). Removal of this outlier does not create significance using the Kruskal-Wallis test (χ^2 =

2.285, df = 2, p-value = 0.319) nor covariance with position in the WIS using Spearman's correlation (ρ = 0.019, S = 2551.6, p-value = 0.930) (Table 8; Fig. 6B and 7B).

Table 8. Spearman's rank correlation results for the number of *Hesperornis* specimens vs. non-binary covariates. The outliers are considered as the red circles in Figs. 4-7 and were qualitatively assessed. The letter S is a test distribution statistic. ρ is the Spearman correlation coefficient. Full results of these non-SDM tests are presented in Supplement S7.

Independent Variable	**Outlier(s) Present?**	**S**	**ρ**	**p-value**
Outcrop Area	Yes	2909.5	0.005	0.980
	No	2297.2	-0.135	0.539
Latitude	Yes	2493.8	0.147	0.472
	No	1402.8	0.208	0.353
Paleolatitude	Yes	2799.8	0.043	0.836
	No	1634.0	0.077	0.732
Position in the WIS	Yes	2650.5	0.094	0.648
	No	2551.6	0.0186	0.930

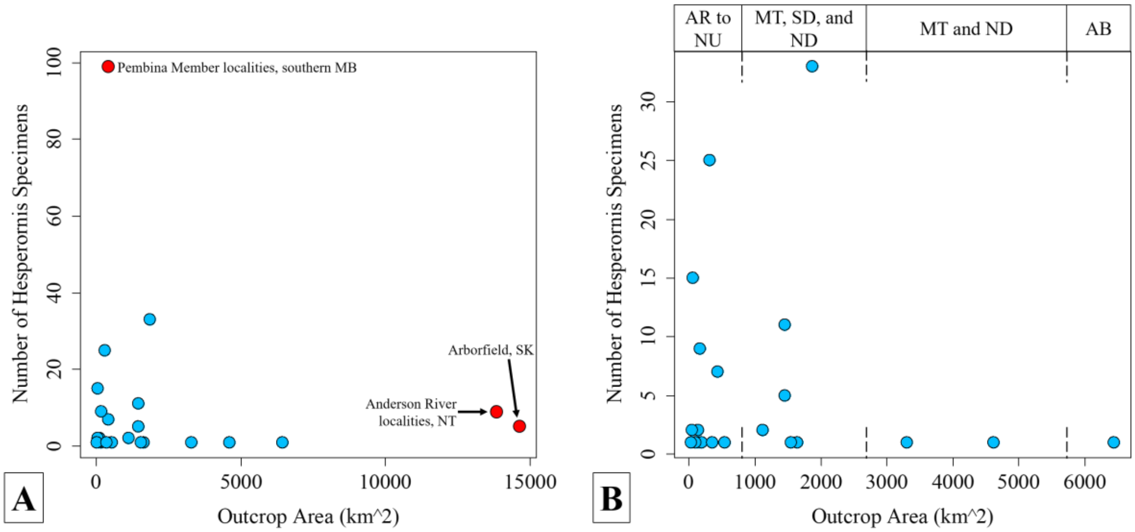

Figure 4. Association of outcrop area (km^2) and the number of *Hesperornis* specimens using Spearman's rank correlation. All locality data are included in A with the red circles indicating substantial outliers that were removed for B. Outcrop area data sources are listed in Supplement S5.

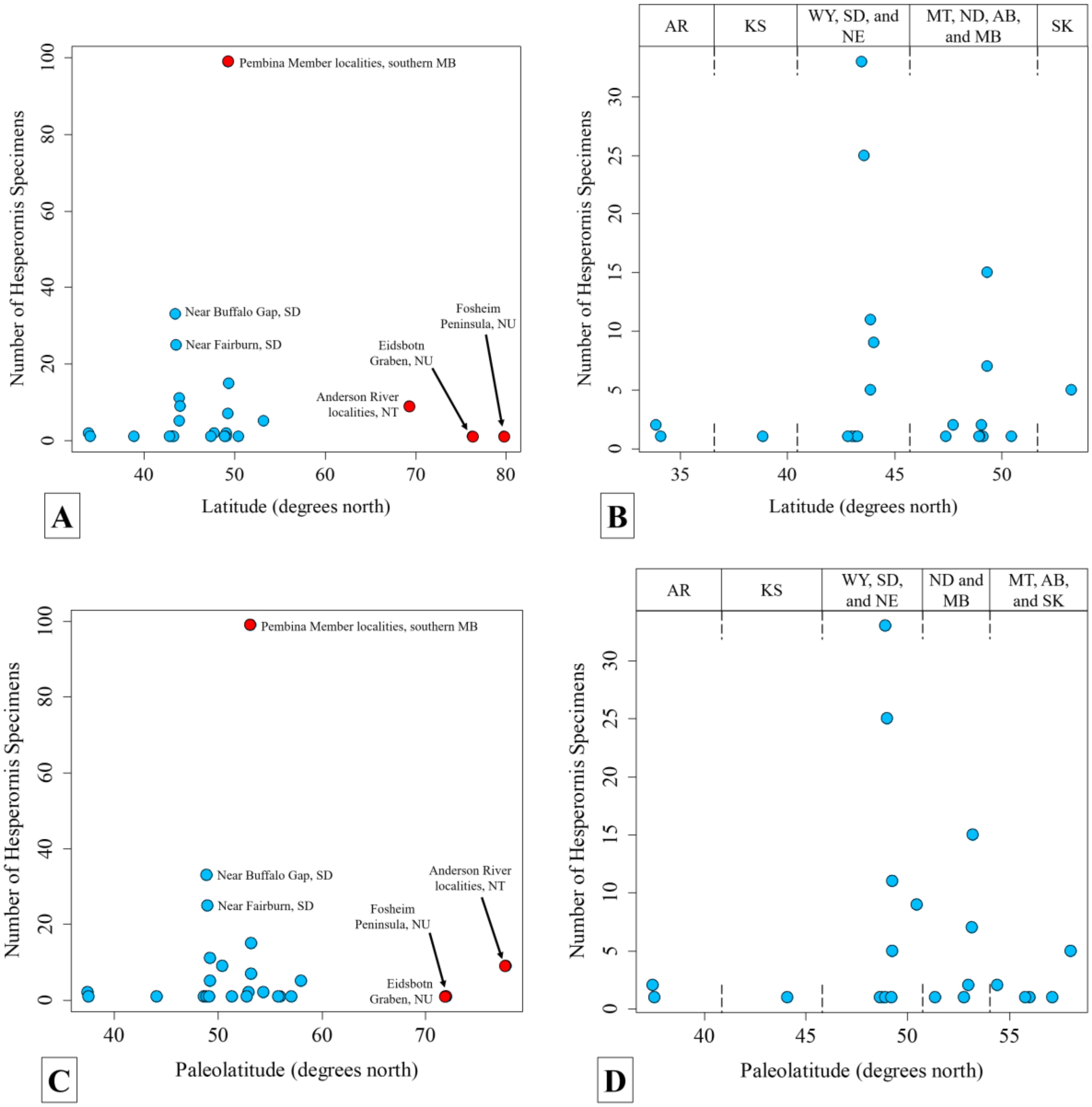

Figure 5. Association of latitude or paleolatitude (°N) and the number of *Hesperornis* specimens using Spearman's rank correlation. Modern latitudes are depicted in A and B. Paleolatitudes at 80 Ma are used in C and D. All locality data are included in A and C with the red circles indicating substantial outliers that were removed for B and D.

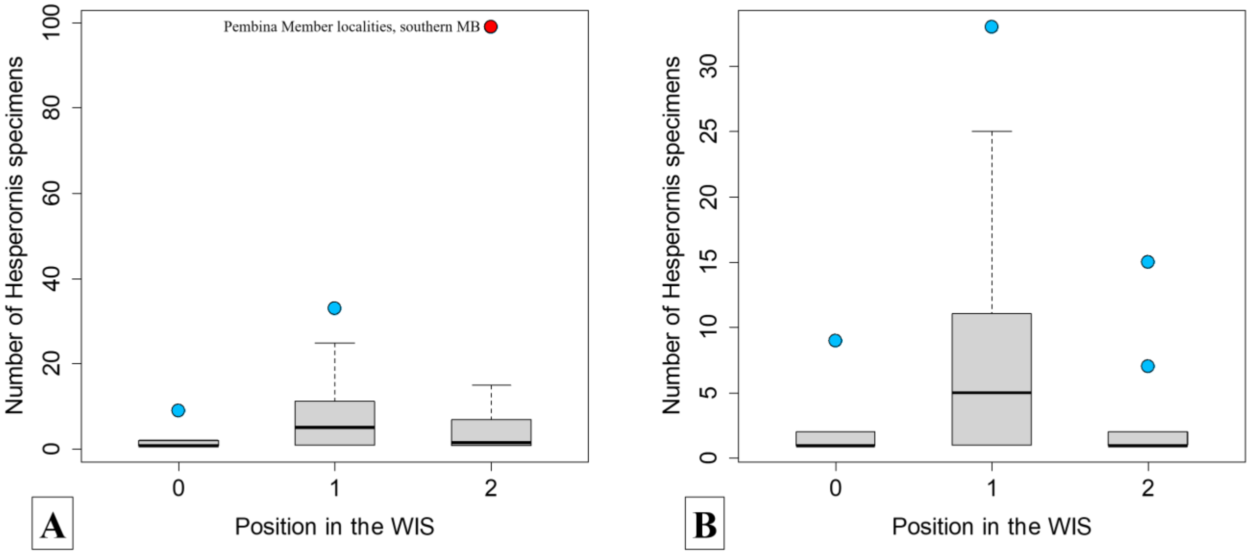

Figure 6. Comparison of the number of *Hesperornis* specimens across the WIS using a Kruskal-Wallis analysis. The western, central, and eastern regions of the WIS are coded as 0, 1, and 2, respectively. The outlier (Pembina Member localities in southern Manitoba) is denoted as a red circle in A. No difference in the number of *Hesperornis* specimens was identified when the outlier is retained in A (χ^2 = 1.751, df = 2, p-value = 0.417) or removed in B (χ^2 = 2.285, df = 2, p-value = 0.319).

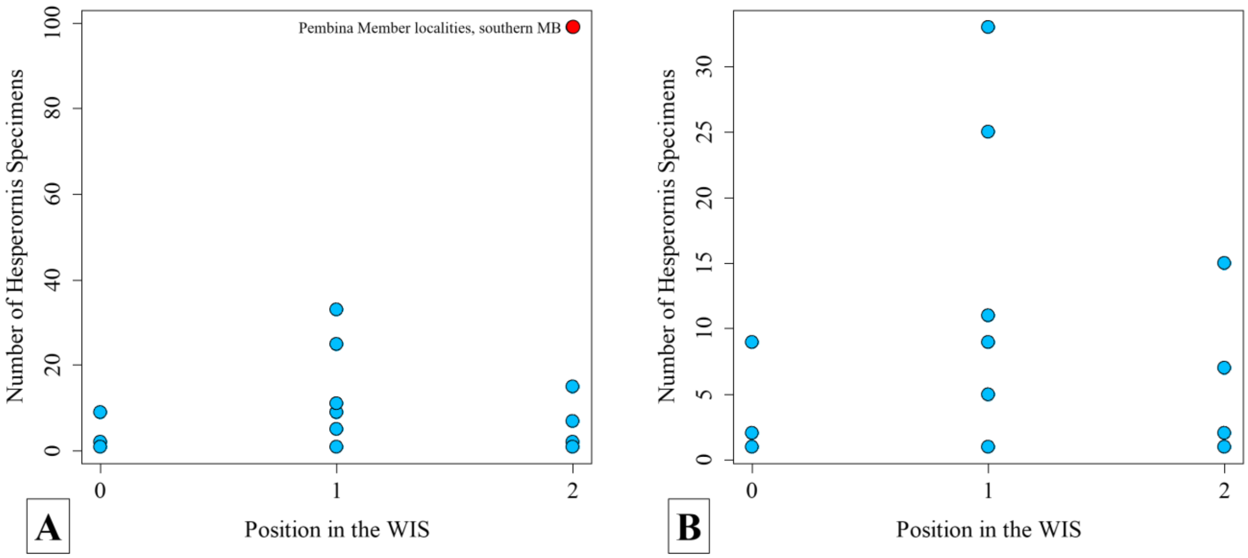

Figure 7. Association of position in the WIS and the number of *Hesperornis* specimens using Spearman's rank correlation. The western, central, and eastern regions of the WIS are coded as 0, 1, and 2, respectively. All locality data are included in A with the red circle indicating an outlier (Pembina Member localities in southern Manitoba) that was removed for B.

DISCUSSION

SDM paleoecological interpretations are limited to relationships between *Hesperornis* (the target species) and other taxa or environmental variables. In this study, *Hesperornis* is interpreted as having strong paleoecological relationships when covariates are supported by both the highest-ranked full dataset GLMs and occupancy models. Covariate groupings for one model type (Table 7) and ecological factors previously hypothesized to influence hesperornithiforms (Tables 1-3) are also discussed.

The current study finds paleolatitude (a continuous covariate) in all seven highest-ranked models (Tables 4, 6, and 7). Positive covariate coefficients indicate that, as paleolatitude increases, the *Hesperornis* occurrence/occupancy probability also increases. This result has several possible paleoecological interpretations. Feduccia (1999) and Rees and Lindgren (2005) hypothesized that hesperornithiforms migrated along the WIS, perhaps breeding in the High Arctic. Northward migration of *Hesperornis* for breeding is supported by a sub-adult (Wilson et al., 2014; 2016) and several small, possibly immature specimens from the High Arctic (Russell, 1967; Bryant, 1983; Nicholls and Russell, 1990; Feduccia, 1999; Hills et al., 1999; Rees and Lindgren, 2005; Wilson et al., 2016). However, multiple small and potentially immature *Hesperornis* specimens have been found in the Manitoba Escarpment of southern Manitoba (Nicholls and Russell, 1990; Aotsuka and Sato, 2016), with potentially more osteologically immature specimens from South Dakota and Manitoba depending on the validity of *Hesperornis macdonaldi* and *H. mengeli* (Martin and Lim, 2002; Aotsuka and Sato, 2016; Bell and Chiappe, 2016). One interpretation is that the presence of potentially immature individuals in Manitoba and South Dakota may not support migration to breed exclusively in the High Artic, but the original breeding hypothesis (Feduccia, 1999; Rees and Lindgren, 2005) could be modified to also include southern Manitoba as a potential breeding area (Aotsuka and Sato, 2016). Unfortunately, bone histology is inconclusive regarding whether *Hesperornis* overwintered in or migrated to the High Arctic (Wilson and Chin, 2014).

Alternatively, the immature *Hesperornis* individuals in southern Manitoba may represent mortality of skeletally immature individuals during migration. Modern fledgling guillemots (*Uria aalge*) have been observed swimming ~200-280 km on average across the Baltic Sea, a journey that begins when they are around 25% of adult body size (Hedgren and Linnman, 1979; Olsson et al., 1999). Perhaps young *Hesperornis* also began their southern migration at an early ontogenetic stage and the high abundance of *Hesperornis* specimens between 48.6-58°N paleolatitude reflects mortality during migration due to geographically restricted oceanographic processes such as shifts in current upwelling strength (reflective of biological productivity), storms, starvation, and exhaustion (e.g., Matović et al., 2017; Jones et al., 2018; Tavares et al., 2020). Mortality in Magellanic penguins (*Spheniscus magellanicus*), for example, is best explained by wave height and atmospheric pressure, both related to storm intensity, and reduction in primary productivity (Tavares et al., 2020). Perhaps some of these same stressors impacted migratory *Hesperornis* resulting in the higher abundance of specimens between southwestern South Dakota and Saskatchewan. This is supported by the hypothesized presence of oceanic fronts and mixing areas in the Central Rocky Mountain/Black Hills region during the late Cenomanian to early Turonian (e.g., Slingerland et al., 1996; Fisher and Hay, 1999; Elderbak and Leckie, 2016; Lockshin et al., 2017) and the Coniacian to early Campanian (Longman et al., 1998). These pre-Campanian fronts and seawater mixing areas also extend into North Dakota, Manitoba, and Saskatchewan (Slingerland et al., 1996; Elderbak and Leckie, 2016; Lockshin et al., 2017). With multiple late Cenomanian to early Campanian studies reporting similar oceanographic mixing hypotheses, it is likely that the same fronts and mixing regions remained throughout the Campanian. Continued mixing of water masses in the Campanian is further supported by the presence of an upwelling zone or oceanographic front in the Denver Basin of Colorado during the early-middle Campanian (Timm and Sonnenberg, 2018).

Another explanation for the positive influence of paleolatitude on *Hesperornis* occurrences is preference of certain paleolatitudes, as indicated by denser *Hesperornis* concentrations, despite a broad paleogeographical range. While Spearman's correlation test did not find a significant linear association between the number of *Hesperornis* specimens and paleolatitude (Table 8), Fig. 4 qualitatively demonstrates that *Hesperornis* specimens are most numerous between 48.6-58°N paleolatitude (43-53°N modern latitude) or southwestern South Dakota to central Saskatchewan. This region includes 222/237 specimens in the dataset (93.7%) (Fig. 1; Supplements S2, S6, and S7). Latitudinal differences in sea surface temperatures could drive increased *Hesperornis* occurrence or occupancy probabilities at these paleolatitudes, with an average sea surface temperature range of 13.7-21.6°C (late middle-late Campanian, southern Canada) to 16-24.2°C (late Campanian non-seep deposits, South Dakota) (He et al., 2005; Dennis et al., 2013; Landman et al., 2018). This temperature range may have been ideal for *Hesperornis* occurrences and may also reflect a region of increased death during migration. Alternatively, the highest abundance can be explained by the oceanic fronts running through Wyoming/South Dakota and southern Canada (Slingerland et al., 1996;

Fisher and Hay, 1999; Elderbak and Leckie, 2016; Lockshin et al., 2017). As regions of high productivity, the mixing zone along the fronts could serve as important feeding grounds for *Hesperornis* similar to how modern Magellanic penguins feed on prey concentrations in these zones (Boersma et al., 2009). The possibility that the influence of paleolatitude on *Hesperornis* occurrences may reflect variation in sampling effort across WIS deposits cannot be discounted at this time. Further study with the current or similar datasets should include covariates that quantify collection bias, perhaps by comparing the total specimens collected over exposure area or the number of active dig years, and covariates for geographic biases such as proximity to cities and towns.

Results from this study found elasmosaurid plesiosaurs present in all highest-ranked occupancy models and full dataset GLMs (Tables 4, 6, and 7). Negative covariate coefficients indicate that the presence of elasmosaurs reduced the probability of occurrence/occupancy for *Hesperornis* and/or that the models support high biogeographical disparity between Elasmosauridae and *Hesperornis*. This implies a possible predator-prey relationship, competitive interactions, or differences in habitat preference. It is unlikely that elasmosaurs exerted a predative pressure on adult *Hesperornis*, despite a large body size, due to their small heads and slender teeth (e.g., Everhart, 2017; Kear et al., 2017). The restricted width between elasmosaur quadrates (15 cm in the Cenomanian and largest WIS elasmosaur *Thalassomedon haningtoni*) and inflexible cranial articulations (Cicimurri and Everhart, 2001; Araújo and Polcyn, 2013) would not enable the swallowing of large adult *Hesperornis*. It is possible that the negative effect elasmosaurids exert on the *Hesperornis* distribution is a competitive pressure. Wilson et al. (2016) hypothesized that hesperornithiforms were generalists who consumed fish, squid, and soft-bodied crustaceans. Similar diets are reported or inferred for most elasmosaurids based on gut contents (fish, cephalopods, crustaceans, other benthic invertebrates, and gastroliths), tooth morphology and wear, and cranial musculature models (Massare, 1987; Cicimurri and Everhart, 2001; McHenry et al., 2005; Araújo and Polcyn, 2013; Everhart, 2017; Kear et al., 2017). One exception is the Campanian-Maastrichtian Aristonectinae (*sensu* Otero, 2016) whose members are inferred filter-feeders (e.g., O'Keefe et al., 2017) and limited to the Southern Hemisphere (O'Gorman; 2019); therefore, aristonectine elasmosaurs would not have likely fed on or competed with hesperornithiforms, which were exclusive to the Northern Hemisphere (Bell and Chiappe, 2016; Tanaka et al., 2018).

Despite ecological similarities and some geographic overlap between Campanian *Hesperornis* and elasmosaurs, it is difficult to provide conclusive evidence for interspecific competition in the fossil record. Competing taxa must share similar feeding ecologies, be contemporaries, live in the same environments, and overlap geographically (Benton, 1996a,b; Ando & Fordyce, 2014; Scott and Anderson, 2021). Both the elasmosaur and *Hesperornis* distributions fit these conditions during the Campanian, but key information is lacking. Supporting evidence for ancient competition is often demonstrated across long time frames (i.e., multiple epochs or ages) and with evidence for character displacement (morphological shifts) or competitive replacement/displacement through negative diversity, abundance, or geographic correlations, or isotopic and microwear analyses on enamel (Feranec et al., 2009; Myers and Lieberman, 2011; Tyler and Leighton, 2011; Ando and Fordyce, 2014; Smith and DeSantis, 2020; Scott and Anderson, 2021).

While a competitive relationship between *Hesperornis* and elasmosaurs is not conclusive, it is possible these taxa shared a complex ecological relationship. Delphinids frequently herd fish into schools that become more accessible for seabirds and some whales are known to steal fish herded by diving seabirds (e.g., Vaughn et al., 2008; Anderwald et al., 2011; Thiebault et al., 2016; Veit and Harrison, 2017). Increases to individual success from group foraging between cetaceans and seabirds likely outweigh competitive pressures (Thiebault et al., 2016; Veit and Harrison, 2017) and this may have been true for elasmosaurs and *Hesperornis*. Alternatively, if *Hesperornis* was capable of diet-switching (*sensu* Wilson et al., 2016) like Adélie penguins (*Pygoscelis adeliae*) during competition with cetaceans (Ainley et al., 2006), a high diversity of prey species in a region may enable *Hesperornis* to reduce competition with elasmosaurs.

The absence of additional evidence for competition or another ecological relationship does not exclude differences in habitat preferences or other abiotic factors that may drive biogeographical disparity patterns between elasmosaurs and *Hesperornis*. Elasmosaurs and *Hesperornis* are most abundant in the cooler waters of mid- to high-paleolatitude localities (i.e., the Northern Interior Faunal Subprovince) (Fig. 8; Nicholls and Russell, 1990). These shared latitudinal distributions, and associated seawater temperature conditions, are unlikely to explain the negative correlation between these taxa. Small-bodied elasmosaurs (both osteologically immature and small-bodied adult individuals) and *Hesperornis* are also known from non-marine and lagoonal settings during the Campanian (e.g., Shufeldt, 1915; Fox, 1974; Sato et al., 2005; DeMar and Breithaupt, 2008; Street, 2020; Campbell et al., 2021) (Supplements S1, S2, and S13) with large-bodied adult and some smaller adult elasmosaurs found further offshore (Sato and Wu, 2006; Campbell et al, 2021). Most occurrences of Elasmosauridae and *Hesperornis*, however, are in marine settings (Carpenter, 1999; Kubo et al., 2012; Wilson et al., 2016; Campbell et al., 2021) (Supplement S2) with Campanian *Hesperornis* abundance highest along the likely locations of oceanographic fronts or mixing zones (see paleolatitude discussion). Congregations of modern seabirds tend to form along mixing and upwelling regions where prey are abundant (e.g., Shealer, 2002; Ballance et al., 2006; Boersma et al., 2009; Fauchald, 2009; Wilson et al., 2019) and the *Hesperornis* occurrences may reflect this trend. Elasmosaurs, by comparison, have a broader distribution across the Campanian WIS (e.g., Carpenter, 1999; Kubo et al., 2012) (Fig. 8). This is not surprising given that elasmosaurs are thought to travel great distances within the WIS to consume gastroliths because those associated with elasmosaur skeletons differ in composition from the surrounding rock matrix or have shapes associated with nearshore to fluvial environments while the elasmosaur skeletons were found in marine deposits (Cicimurri and Everhart, 2001; Kubo et al., 2012). It is possible that elasmosaurs regularly traveled between different regions of the WIS to feed, but this is currently unknown. Perhaps the negative correlation between *Hesperornis* and elasmosaurs is related to habitat distributional patterns with elasmosaurs lacking preferred regions outside of mid- to high-paleolatitudes and *Hesperornis* congregating around oceanic fronts.

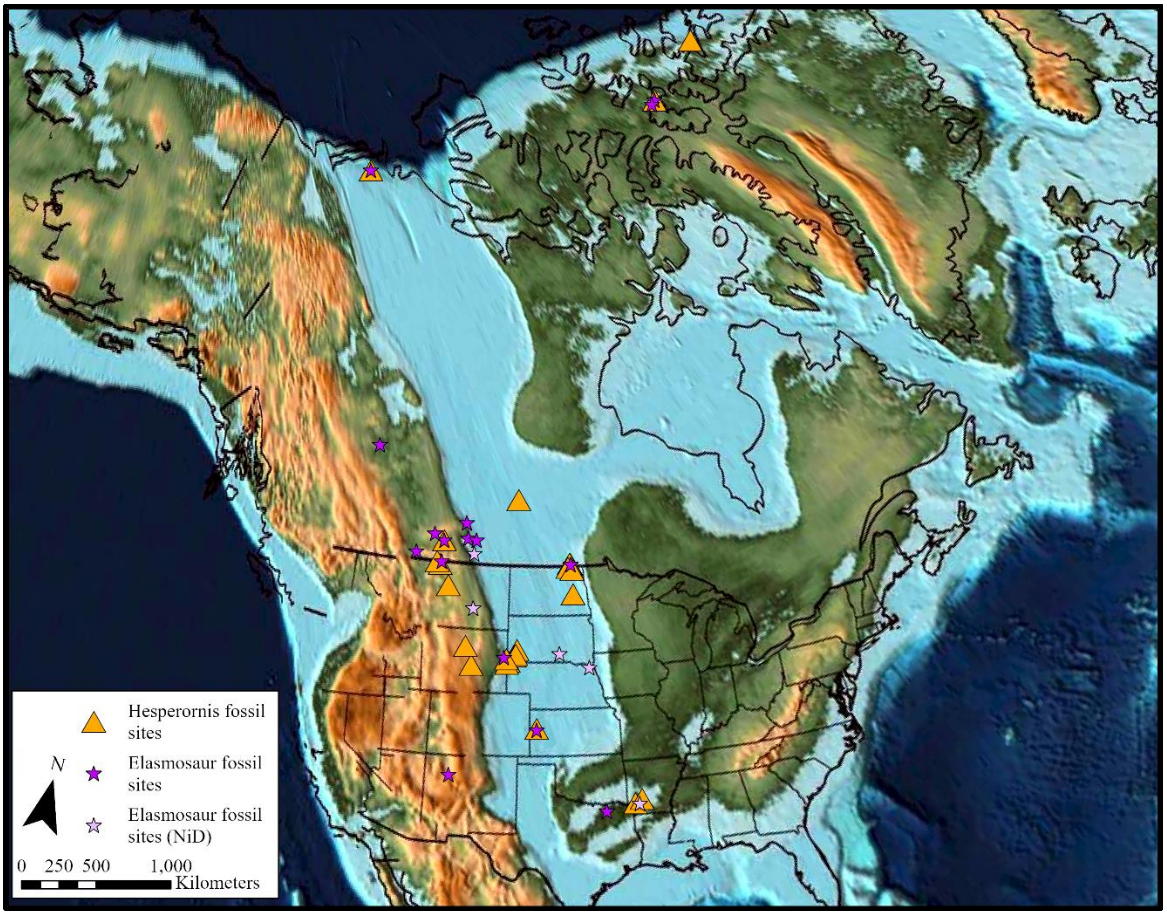

Figure 8. Distribution of Campanian *Hesperornis* and elasmosaurs in the WIS. Campanian sites are reconstructed to the early middle Campanian (80 Ma) and depicted using an 80 Ma paleogeographic map (modified from Scotese, 2016). Symbols representing fossil localities are not to scale. Data were obtained from the Paleobiology Database, museum collections records, and published literature (Supplements S2 and S13). NiD identifies elasmosaur specimens that were not included in the current dataset because they were isolated occurrences without a vertebrate community (Supplement S13).

Covariate Groupings from One Model Type

It is possible that the full dataset GLM or occupancy model covariate groupings could reflect reality rather than covariate groupings shared by both model types (Table 7). In the full dataset GLM grouping, all covariates (Elasmosauridae + *Toxochelys* + paleolatitude) have a positive influence on *Hesperornis* occurrences except for Elasmosauridae. Elasmosauridae and paleolatitude likely have the same relationship to *Hesperornis* as discussed previously, but it is unclear how *Toxochelys* relates to *Hesperornis*, if at all. Current dietary interpretations for *Toxochelys* describe a consumer of fish, hard-shelled invertebrates, and soft-bodied organisms, supporting a generalist diet like *Hesperornis* and elasmosaurs. This is based on fish-bearing coprolites associated with UCM 70738 and snout emargination on other skulls (Carpenter, 2006; Carrino, 2007). An overlap in diet could imply competition, but the positive impact of *Toxochelys* on *Hesperornis* occurrences from the full dataset GLMs negates this conclusion. Alternatively, *Toxochelys* could be preferred to *Hesperornis* as prey of larger predatory species such as *Tylosaurus* and *Squalicorax* as *Toxochelys* has been found as stomach contents and with bite marks (Druckenmiller et al., 1993; Schwimmer et al., 1997; Martin and Bjork, 1987; Bell and Barnes, 2007; Everhart et al., 2013). A preference for *Toxochelys* as food would increase the probability of *Hesperornis* occurrence with reduction of predation pressure on the latter. However, despite partial geographic overlap in Manitoba, South Dakota, Kansas, and Arkansas (Gentry and Ebersole, 2018) (Fig. 1), there is no clear biogeographic pattern or biological explanation for why the full dataset GLMs support higher *Hesperornis* occurrence probabilities when *Toxochelys* was present. Any effects of *Toxochelys*-elasmosaur interactions on *Hesperornis* occurrences are equally unclear. Although untested, perhaps these three generalist taxa co-occurred because all exhibited dietary flexibility through diet-switching.

The occupancy model covariate grouping (Table 7) is divided into two parts with potential influence on the *Hesperornis* distribution. Elasmosaurs, paleolatitude, and WIS position were modeled as important to the probability of *Hesperornis* occupancy while the detection probability was influenced by carbonate rocks and outcrop area. Of the five covariates, only paleolatitude and WIS position have a positive association with *Hesperornis*. For occupancy probabilities, elasmosaurs, paleolatitude, and the elasmosaur-paleolatitude interaction likely had the same effects as discussed above. Abundance of *Hesperornis* did not significantly vary west to east across the WIS (Figs. 6-7; Table 8), likely reflecting no preference by *Hesperornis* and the lack of preservational bias among these regions. The WIS position covariate was also not incorporated into any highest-ranked full dataset GLMs (Table 4; Supplements S7 and S9), further supporting this conclusion. The five highest-ranked occupancy models, however, detected a positive association of WIS position and *Hesperornis* occurrences. This association is likely not caused by differences in *Hesperornis* occurrence counts between regions because all are nearly equivalent between the west (3), middle (4), and east (4). Rather, the occupancy models may be detecting the interaction between WIS position and other occupancy probability covariates in the model. The Elasmosauridae-WIS position interaction is not likely to affect the *Hesperornis* distribution because elasmosaurs do not appear to have a strong preference for any west to east region. It is more likely that the interaction between WIS position and paleolatitude influenced *Hesperornis* occurrence probabilities. The interaction may manifest as the concentration of *Hesperornis* occurrences in southwestern South Dakota (middle WIS) and Manitoba (eastern WIS), along the mixing region of southern and northern water masses, within 48.6-58°N paleolatitude where the *Hesperornis* specimen count is most numerous (222/237 specimens in the dataset) (Figs. 5-7).

The occupancy models predict that carbonate decreases the probability of *Hesperornis* detection, which likely reflects decreasing eustacy during the middle to late Campanian (e.g., Haq et al., 1987; Müller et al., 2008; Blakey, 2014). During the early Campanian, chalk and other calcareous deposits stretched from the Cretaceous Gulf Coast to the Dakotas and potentially to the Manitoba Escarpment (represented by the upper Boyne Member of the Carlile Formation) along the middle to eastern WIS, but after the early Campanian, ocean-derived carbonates disappear from the WIS as sea levels decrease (Shurr and Reiskind, 1984; Roberts and Kirschbaum, 1995; Bamburak et al., 2013; Shaw et al., 2017). This is reflected in the current full dataset where only two of the early Campanian carbonate-bearing sites are in South Dakota and Kansas while the other four early Campanian carbonate-bearing sites are located along the Cretaceous Gulf Coast in modern Texas. The 11 middle-late Campanian carbonate-bearing sites also fall along the Cretaceous Gulf Coast in Texas and Arkansas. *Hesperornis* is present at 4/17 carbonate-bearing sites in the full dataset with one occurrence each in Kansas and South Dakota (early Campanian) and two occurrences in Arkansas (middle-late Campanian).

In the occupancy model data, only 4/22 total sites bear carbonate lithologies, and *Hesperornis* is present at only one of these sites: the early Campanian Niobrara deposits in Kansas. The *Hesperornis*- and carbonate-bearing areas in Arkansas were not included in the occupancy models because the number of localities in Hempstead and Clark

Counties are unknown. Regardless, if these two combined sites were included in the occupancy models, the number of *Hesperornis*- and carbonate-bearing sites (3/22) would remain much smaller than *Hesperornis*- and mudrock-bearing sites (8/22). Therefore, it remains likely that eustatic shifts drive the apparent decrease in *Hesperornis* detection when carbonate is present.

Outcrop area does not have a linear relationship with *Hesperornis* specimen counts (Table 8; Fig. 4), but outcrop area is present in 4/5 highest-ranked occupancy models. In these models, outcrop area has a negative association with *Hesperornis* occurrences implying that larger outcrop areas decrease the probability of *Hesperornis* occupancy. This result is reasonable when compared to Fig. 4, which shows that most *Hesperornis* specimens came from < 2000 km^2 outcrop areas. Perhaps larger outcrop areas are not as heavily or evenly sampled and *Hesperornis* specimens are less likely to be observed. Larger outcrop areas may also not be completely sampled or were unevenly sampled because of their broader geographic size compared to small rock outcrops. It is unlikely that differences in outcrop area among lithologies influenced *Hesperornis* occurrences. *Hesperornis* specimens have been found primarily in mudrock deposits (Supplements S1 and S2) which have higher rates of sedimentation and may appear less fossiliferous than carbonaceous deposits. Sedimentation rates for the Sharon Springs Formation (shale) and the Campanian portion of the Niobrara Formation (marl to chalk) have been estimated at 10-104 m/myr (1-10.4 cm/kyr) and 9-26 m/myr (0.9-2.6 cm/kyr), respectively (Carpenter, 2006; Locklair and Sageman, 2008). Unfortunately, outcrop area trends in the occupancy models cannot be verified by the full dataset GLMs at this time due to model fitting issues that usually occur when outcrop area is an included covariate.

Perhaps with better resolution on preserved outcrop in North America, a possible influence on *Hesperornis* occurrences could also be identified from the full dataset GLMs.

Outcrop area is likely among the most important determinants of detection probability because this property provides the total amount of space available for sampling. This information helps characterize biases including collection effort, survey completeness for an outcrop, and variable exposure (e.g., Crampton et al., 2003; Peters and Heim, 2010). Unfortunately, outcrop area is often difficult to estimate at the level of rock exposure for a locality. Both Liow (2013) and this study encountered issues with precise measures of outcrop area because these data are typically not published online and may not have been measured. The lack of measurement is particularly challenging for older localities where determining outcrop size was not the purpose of the excavation (e.g., sites collected by O. C. Marsh and E. D. Cope) or the site may no longer be accessible (e.g., demolished road cuts or the now-submerged Bailey Island of the Missouri River in South Dakota) (Welles and Bump, 1949; pers. obs.). While outcrop area estimation from geologic maps is a useful proxy, these estimates do not typically account for recent geological cover (e.g., topsoil, alluvium, or glacial till) and human development (Uhen and Pyenson, 2007; Dunhill, 2011; 2012). Part of this problem can be circumvented by obtaining estimates using remote sensing and GIS to map the true rock exposure area rather than mapped geologic unit areas (Dunhill, 2011; 2012). Alternatively, for localities whose dimensions are not provided in published literature, museum/institution records can be consulted to see how individual sites were sampled, if recorded. Both options, however, are quite time-intensive and would likely require numerous research teams/projects at smaller scales before true outcrop exposure area analysis at the continental scale. For example, inquiry regarding the size of Campanian deposits for this study would require information on 61 sites (including 21 localities of 2-31 smaller sites each) and a search through the records of at least 26 institutions. If information on outcrop exposure area is lacking in collections records, use of remote sensing and GIS data (*sensu* Dunhill, 2011; 2012), or personal measurement of outcrops would be necessary if the outcrops remain accessible. Georeferenced coordinate uncertainty could constrain outcrop area from geologic maps to a more finite area around a known fossil locality. This restriction may better reflect true rock exposure area, but further tests are needed.

Other Covariates of Note

Polycotylids are another group of plesiosaurs in the WIS, but these taxa possess a shorter neck and longer skull unlike the long neck and short skull length characterizing elasmosaurs. Martin et al. (2016) hypothesized that a polycotylid plesiosaur attempted to eat a juvenile *Hesperornis* based on tooth marks discovered on an adult *Hesperornis* tibiotarsus (YPM VPPU 017208.D) in South Dakota. Since these bite marks show evidence of healing, they likely reflect an act of predation and not scavenging. Campanian polycotylids could reach 6-7 m long with heads around 1 m long (Schumacher and Martin, 2016; Everhart, 2017). While perhaps not large enough to feed on adult *Hesperornis regalis*, *H. lumgairi*, and *H. gracilis* (≤ 1.9-2.0 m in length), polycotylids may have been able to eat juveniles or smaller *Hesperornis* species such as *H. macdonaldi* (~0.8 m long) (size estimates based on Martin and Lim, 2002; Wilson et al., 2011; Aotsuka and Sato, 2016). In this study, however, polycotylid plesiosaurs did not appear as a covariate in any of the seven highest-ranked models among all model types (Table 7) and occurrences outside of the highest-ranked models had variable positive or negative covariate coefficients. Together, these results indicate that polycotylids likely had minimal impact on *Hesperornis* occurrences. Consequently, YPM VPPU 017208.D may represent a rare attack on *Hesperornis* rather than *Hesperornis* being the preferred prey of polycotylids. Additionally, stomach contents of polycotylids provide evidence of feeding on teleosts and ammonites, and their tooth morphology suggests a generalist diet such as fish and squid (Massare, 1987; Sato and Tanabe, 1998; Cicimurri and Everhart, 2001; Janzic, 2006).

Tylosaurus, a large mosasaur capable of reaching 13-14 m in length (Everhart, 2017), was hypothesized to be an opportunistic predator by Martin and Bjork (1987) based on stomach contents of SDSM 10439 that include *Hesperornis* sp. (Table 1). The wide variety of vertebrate taxa found as stomach contents from this specimen and other *Tylosaurus* individuals supports their hypothesis (e.g., Everhart, 2004a; Bell and Barnes, 2007). As a covariate in the distribution of *Hesperornis*, *Tylosaurus* was found in only one of the highest-ranked occupancy models (Table 6; Supplements S7 and S12) and likely reflects noise in the models. This indicates that *Tylosaurus* is unlikely to have exerted a strong influence, predative or otherwise, on *Hesperornis* despite occasionally feeding on the latter. Model results from this study do not refute the hypothesis that *Tylosaurus* was opportunistic (e.g., Martin and Bjork, 1984; Everhart, 2004a; Bell and Barnes, 2007) rather than preying on specific taxa.

Martin and Tate (1976) hypothesized that *Fumicollis hoffmani* (*sensu* Bell and Chiappe, 2015) consumed the teleost *Enchodus* and other fish based on coprolites/colonites associated with UNSM 20030 from Kansas (Table 1) (Martin and Tate, 1976; Bell and Chiappe, 2015). *Enchodus* could have been small enough to be consumed by *Hesperornis*. The largest *Enchodus* species (*E. petrosus*) reached 1.5 m long, but smaller individuals and other *Enchodus* species could be prey for a large hesperornithiform (Martin and Tate, 1976; Bell and Chiappe, 2015; Everhart, 2017). The largest WIS species of *Hesperornis* (≤ 1.9-2.0 m long) were bigger than *F. hoffmani* (~1.1-1.3 m long) (based on measurements in Wilson et al., 2011; Bell and Chiappe, 2015; Aotsuka and Sato, 2016); therefore, these *Hesperornis* species could also consume smaller *Enchodus* individuals. However, *Enchodus* was present in none of highest-ranked models (Tables 4, 6, and 7), which indicates that *Enchodus* was not a major food source, or it may have been seasonally or regionally consumed by *Hesperornis*. This result is not surprising given the ubiquitous nature of *Enchodus* in the WIS (e.g., Goody, 1976; Martin et al., 1998; Cavin et al., 2012; Supplement S2) and the generalist diet and potentially migratory behavior of *Hesperornis* (Feduccia, 1999; Rees and Lindgren, 2005; Wilson et al., 2016). Modern seabirds often search vast distances of water for prey patches, with these patches behaving dynamically in geographic location and areal extents (e.g., Shealer, 2002; Vlietstra 2005; Boersma et al., 2009; Fauchald, 2009). These fluctuations can lead to migration between feeding areas and/or prey-switching. Seasonal or interannual environmental shifts and the distance of prey aggregations from seabird breeding colonies also influence the prey species targeted (e.g., Ainley et al., 1996; Vlietstra, 2005; Wells et al., 2017).

Hanks and Shimada (2002) and Shimada and Hanks (2020) hypothesized that hesperornithiforms were prey of the generalist shark *Squalicorax* based on *Squalicorax* cf. *falcatus* bite marks on a partial hesperornithiform tibiotarsus (SMM P2001.12.10) (Table 1). *Squalicorax* species could reach lengths of 2.0-4.8 m and lived throughout the WIS with the most Campanian occurrences limited to southern Canada and lower latitudes (e.g., Nicholls and Russell, 1990; Schwimmer et al., 1997; Shimada and Cicimurri, 2006) except for one occurrence on Devon Island, Nunavut in the High Arctic (Chin et al., 2008). *Squalicorax* had a tooth morphology resembling tiger sharks (*Galeocerdo cuvier*) who feed indiscriminately and are known to eat seabirds and carrion (e.g., Lowe et al., 1996; Compagno, 2001; Simpfendorfer et al., 2001; Dicken et al., 2017). *Squalicorax* species are probable scavengers or opportunists with evidence of feeding on traditional marine reptile taxa, dinosaurs, fish, pterosaurs, starfish, and hesperornithiforms (e.g., Druckenmiller et al., 1993; Schwimmer et al., 1997; Neumann, 2000; Everhart, 2004b; Shimada and Cicimurri, 2005; Ehret and Harrell, 2018; Shimada and Hanks, 2020). Despite feeding on hesperornithiforms, *Squalicorax* is unlikely to affect the *Hesperornis* distribution because, like the *Tylosaurus* and *Platecarpus* covariates, *Squalicorax* only appears in one of the highest-ranked occupancy models and is not a shared covariate in most of these models (Table 6).

Model Comparison and Discussion

Each SDM type has advantages and disadvantages. For GLMs and occupancy models, these differences are largely sampling and the detection probability estimation (Table 9). Unlike occupancy models, GLMs do not estimate the detection probability (i.e., the probability of observing the target species) and do not provide unbiased occupancy probability estimates (i.e., the probability that the target species is present) for a site unless the species is always detected at all sites where it is present (Pearson, 2010; Guillera-Arroita et al., 2015). Unless this condition is met, occupancy probabilities for GLMs (exclusive of occupancy models) cannot be separated from detection probabilities (e.g., Guillera-Arroita et al. 2015; MacKenzie et al., 2018). In this way, occupancy models are more advantageous than GLMs because these models simultaneously model occupancy and detection probabilities.

On the other hand, GLMs are advantageous because these models can include information from single-sample and multi-sample sites for a combined higher site count. Detection probability estimation in occupancy modeling requires site detection histories built using multiple samples from each site. Most fossil sites have not been sampled or collected for determining the detection history which would necessitate repeated collection expeditions or sampling of multiple beds within a single time interval at one locality (Liow, 2013). Rather, paleontological localities are often only sampled once (e.g., Meyer, 1974; Kass, 1999; Sato, 2003; Bell et al., 2014), while other localities and regions are repeatedly sampled (e.g., Bardack, 1968; Lillegraven and McKenna, 1986; Case, 1987; Brinkman, 1990; Brinkman et al., 2005; DeMar and Breithaupt, 2008; Aotsuka and Sato, 2016). Detailed information on collection practices is typically unavailable in the published literature with fossil assemblages often combined into broad geological units (e.g., Case, 1987; Hoganson et al., 1996; Eaton et al., 1999; Peng et al., 2001). In this study, the larger GLM site availability is demonstrated with 61 localities, but only 22 of these localities (36.1%) were repeatedly sampled regions appropriate for occupancy modeling.

Table 9. Advantages and disadvantages of model types used.

	Advantages	**Disadvantages**
Full Dataset GLMs (And Other non-Occupancy Model Presence/Absence Methods)	• Require less data than occupancy models (i.e., do not need site detection histories) • Do not require multiple samples per site → more sites available for sampling	• Cannot estimate probability of detection → biased occupancy estimates
Occupancy Models (An Extension of GLMs)	• Account for detection probability → unbiased occupancy estimates	• Require multiple samples per site → fewer sites available for sampling

Ultimately, including both GLMs and occupancy models in a single study offers comparison among techniques and incorporate different data types. Agreement in individual covariates or covariate groupings across model types offers the most support for covariate/covariate grouping relationships with the target species. The agreement shows that, despite differing in total site or survey count, the models can inform on overall ecological patterns. Covariates present in multiple high-ranking models (ΔAIC $\leq$ 2) of one model type (e.g., Table 7) indicate that those covariates may be important for estimating occurrence/occupancy or detection probabilities for the target species at a given locality. Covariates that are irregularly included in models (e.g., Actinopterygii and *Clidastes* in the full dataset GLMs or *Platecarpus*, *Tylosaurus*, and *Squalicorax* in the occupancy models) (Tables 4 and 6; Supplements S7, S9, and S12) are unlikely to be important to the target species because they are only explaining some of the variation in that model whereas the covariates consistently in the highest-ranked models explain more variation.

The SDMs generated in this study were successfully run for the Campanian WIS ecosystem. For the highest-ranked full dataset GLMs, this was demonstrated when these models were found as significant compared to the null model (Table 4; Supplements S7 and S9). For the occupancy models, the global model was assessed for fit and found to have a non-significant χ^2 statistic compared to the bootstrapped χ^2 value (p-value = 0.611) (Supplements S7 and S12). This indicates that the model and more parsimonious models should describe the data well. For the current study, the global occupancy model was represented by the following occupancy covariates: the larger taxonomic groups (Table 2), StdPaleolatitude, and WIS position. The detection covariates for this model were the three sedimentary lithologies and StdOutcrop area. The highest-ranked occupancy models also returned observed χ^2 values less than the bootstrapped χ^2 values (Supplements S7 and S12) indicating that these models appropriately fit the data.

Overall, the SDMs were useful for elucidating ecological patterns in the WIS. They determined that paleolatitude strongly influenced *Hesperornis* occurrences and enabled quantitative testing of taxa hypothesized to have ecological interactions with hesperornithiforms based on qualitative fossil evidence alone, namely *Tylosaurus*, *Squalicorax*, polycotylids, and *Enchodus*. One downside is that they can identify covariates as important to the target species that, upon further examination, might be in-contrast with some paleobiogeographical, sedimentological, and ecological data and not as relevant to the species of interest (e.g., elasmosaurs, *Toxochelys*, and carbonate for

Hesperornis occurrences). Future analyses using fewer and more targeted covariates will likely prune out unimportant covariates to result in models more accurate to the ecosystem. There also remains some unexplained variation in the data according to full dataset GLM results. These models have an average explained variation or deviance of 0.535 (range = 0.427-0.622) (Table 4; Supplements S7 and S9). This indicates that 37.8-57.3% of the variation is not included in current full dataset GLMs. Additional variation in *Hesperornis* occurrence data may be explained by testing other occupancy and detection covariates not yet considered (see Future Directions).

There are several potential taphonomic issues with the current SDMs that must be addressed. The models evaluate the ecological factors that may have influenced *Hesperornis* occurrences across the Campanian, a geologic age with a duration of 11.5 million years (Cohen et al., 2013; updated). Compared to other geologic ages of the Late Cretaceous, the Campanian lasted nearly twice as long as the second longest geologic age (Cenomanian) and over four times longer than the shortest geologic age (Santonian) (Cohen et al., 2013, updated), which could create stronger time-averaging problems. The issue is partially addressed by using some combined sites that were from the same rock unit and time of deposition (i.e., early, middle, and late Campanian). These Campanian subdivisions are approximately 3.2, 4.3, and 4.2 million years in duration, respectively (Ogg and Hinnov, 2012). Despite being a better fit to other Late Cretaceous geologic age durations, Campanian subdivisions cannot be used for evaluating *Hesperornis* occurrences because these divisions are limited by site sample size (Supplement S3) and are likely not as reliable as SDMs using the entire Campanian.

Preservational bias may have played a role in creating high abundance of *Hesperornis* between 43-53°N modern latitude because Campanian-aged rocks are largely absent north of ~53°N modern latitude along the northern WIS either by low outcrop exposure or preservation (Stott et al., 1993; Fenton et al., 2013; Prior et al., 2013). Additionally, Campanian-aged deposits along the eastern shoreline of WIS have eroded away (e.g., Slattery et al., 2015), which leads to information loss for *Hesperornis* occurrences. Fortunately for the models, these erosional issues affect all taxa and not just *Hesperornis*, so inferences regarding ecological relationships between *Hesperornis* and other taxa should be unaffected in the models.

Potential transport of *Hesperornis* bones from the site of death by currents has not been modeled in this study. The dominance of hindlimb, pelvic, or vertebral elements from *Hesperornis* in the Campanian WIS (Carpenter, 2006; Aotsuka and Sato, 2016; Bell and Chiappe, 2016) has been interpreted by Carpenter (2006) as evidence of post-mortem disarticulation while floating. This potential for transport could be addressed in future studies by including a covariate for skeletal completeness as a proxy for the transport time or disarticulation through scavenging or predation.

The occupancy models in this study inform on taphonomic bias using the detection history data to better characterize overall paleocommunities in an area. These models explicitly account for differential effects of lithology and outcrop area on the detectability of *Hesperornis*. Only carbonate was considered as important to *Hesperornis* detectability in the occupancy models among lithologies, but this may be an artifact of regression during the middle and late Campanian. The full dataset GLMs do not explicitly account for taphonomic issues because outcrop area, a covariate that only affects detection probabilities, could not be modeled and the effect of lithology cannot be segregated between occupancy and detection probabilities. Inclusion of additional covariates that exclusively describe taphonomic bias (e.g., skeletal completeness and erosional or weathering proxies) could avoid the problem faced by lithological covariates in the GLMs.

CONCLUSIONS

Paleontological SDMs have focused on non-marine taxa and marine invertebrates, with only two studies examining the past distribution of marine vertebrates. No SDM studies have examined extinct marine vertebrates from the Late Cretaceous, leaving a gap in paleontological SDM applications and research. The current study uses GLMs and occupancy models to determine the ecological covariates that most explain the distribution of *Hesperornis*, an extinct flightless seabird for which several paleoecological interpretations have been proposed, but none have been quantitatively evaluated.

This study has two objectives: 1) Identify the ecological controls on the distribution of *Hesperornis* and 2) Test the applicability of SDMs in the WIS. The strongest ecological controls are elasmosaurs and paleolatitude. Elasmosaurs may negatively influence the *Hesperornis* distribution through competition or the model results for elasmosaurs may represent different habitat preferences from *Hesperornis*. Paleolatitude may reflect *Hesperornis* migration behavior, migration mortality, or true environmental preference. The negative association between carbonate lithologies and *Hesperornis* likely reflects changes in eustacy during the middle to late Campanian rather than an influence on the probability of *Hesperornis* detectability. No support is provided by the highest-ranked models (ΔAIC ≤ 2) for two taxa previously hypothesized to prey upon *Hesperornis*, namely *Tylosaurus* and Polycotylidae (Martin and Bjork, 1987; Martin et al., 2016), for *Enchodus* as preferred prey of *Hesperornis*, or for *Squalicorax* as a predator or scavenger of *Hesperornis*. *Hesperornis* did not prefer a particular west to east region of the WIS, but where the genus occurred may be related to an interaction between WIS position and paleolatitude. This may be reflected in higher abundance of *Hesperornis* along hypothesized mixing zones and oceanic fronts within the WIS (see Discussion). Lastly, higher detectability of *Hesperornis* specimens may be limited to smaller outcrop area sizes, but more testing is needed.

Species distribution modeling is useful to model WIS taxa by providing quantitative insight into ecological patterns with more information obtained from comparing SDM techniques (e.g., GLMs and occupancy models). Maximum likelihood estimation using ΔAIC enables comparison of model support to determine the combination of covariates that is most explained by the current *Hesperornis* dataset. Modeling software for SDMs (e.g., R and PRESENCE) makes it easy to simultaneously compare numerous variables from environmental and biological elements of the WIS such as endemic taxa, lithologies, and paleogeographical information. The software also provides detailed model outputs to describe models and diagnose problems. GLMs and occupancy models are both useful to model extinct taxa because they incorporate different data (i.e., more sites in GLMs and the detection history in occupancy models). Use of GLMs with datasets meant to match occupancy models is not recommended because these reduced dataset GLMs have examine fewer sites, return higher error rates, and do not converge on an overall covariate grouping.

Future Directions and Applications for Paleontological Analyses

The potential for customizing occupancy models and GLMs leaves many avenues for expanding current analyses. There remain many additional occupancy/occurrence covariates to consider for WIS studies: distance from paleoshoreline, inferred water depth, proximity to river mouths, models of WIS circulation or sea surface temperatures, lithological sub-categories and features, invertebrate occurrences, and size classes of included taxa. Other covariates can be used to account for more sampling/collection and detection biases: proximity to areas of high human development, bedding plane area, researcher/collection bias for sampling effort, research effort as gauged by publication or author counts per stratigraphic/chronologic unit, land use, and taphonomy, including skeletal completeness (e.g., Uhen and Pyenson, 2007; Dunhill, 2011; Dunhill et al., 2012; Benton et al., 2013; Vilhena and Smith, 2013). Proximity to areas of higher human development, which can be characterized by location of outcrops or human population size, may act as a proxy for ease of access to a site (e.g., Uhen and Pyenson, 2007; Dunhill et al., 2012). Bedding plane size can reflect preservational or sampling biases in the presence of bedding surface heterogeneity (Liow, 2013; Marenco and Hagadorn, 2019). It is currently unknown if the size of the site buffer impacts model results in this study. Future studies should experiment with different site buffer dimensions using real and simulated data to evaluate if the choice of modeling buffer size creates or reduces significant sampling bias.

The methods used in this study could easily be applied in new regions of the world and to different time periods. The current *Hesperornis*-focused dataset could be transformed to emphasize a different taxon (e.g., Mosasauridae) with *Hesperornis* and Hesperornithiformes becoming covariates. Further studies using the current dataset, with more covariate characterization of WIS paleoenvironmental conditions, could examine species co-occurrence and predict community occupancy rather than occupancy for a single taxon (e.g., Zipkin et al., 2010; Pollock et al., 2014).

REFERENCES

Agresti, A. 2013. Categorical Data Analysis (Third Edition). Wiley Series in Probability and Statistics. John Wiley & Sons, Inc., Hoboken, New Jersey, 714 pp.

Ainley, D. G., G. Ballard, and K. M. Dugger. 2006. Competition among penguins and cetaceans reveals trophic cascades in the Western Ross Sea, Antarctica. Ecology 87(8):2080-2093.

Ainley, D. G., L. B. Spear, S. G. Allen, and C. A. Ribic. 1996. Temporal and spatial patterns in the diet of the common murre in California waters. The Condor 98(4):691-705.

Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle; pp. 267-281 in B. N. Petrov and F. Caski (eds.), Proceeding of the Second International Symposium on Informational Theory, Akadémiai Kiadó, Budapest, September 2-8, 1971.

Akaike, H. 1974. A new look at the statistical model identification. IEEE Transactions on Automatic Control AC-19(6):716-723.

Anderwald, P., P. G. H. Evans, L. Gygax, and A. R. Hoelzel. 2011. Role of feeding strategies in seabird–minke whale associations. Marine Ecology Progress Series 424:219-227.

Ando, T., and R. E. Fordyce. 2014. Evolutionary drivers for flightless, wing-propelled divers in the Northern and Southern Hemispheres. Palaeogeography, Palaeoclimatology, Palaeoecology 400:50-61.

Aotsuka, K., and T. Sato. 2016. Hesperornithiformes (Aves: Ornithurae) from the Upper

Cretaceous Pierre Shale, Southern Manitoba, Canada. Cretaceous Research 63:154-169.

Araújo, R., and M. J. Polcyn. 2013. A biomechanical analysis of the skull and adductor chamber muscles in the Late Cretaceous plesiosaur *Libonectes*. Palaeontologica Electronica 16(2:10A):25 pp.

Armstrong, R. A. 2014. When to use the Bonferroni correction. Ophthalmic & Physiological Optics 34(5):502–508.

Artusi, R., P. Verderio, and E. Marubini. 2002. Bravais-Pearson and Spearman correlation coefficients: meaning, test of hypothesis and confidence interval. The International Journal of Biological Markers 17(2):148-151.

Babyak, M. A. 2004. What you see may not be what you get: A brief, nontechnical introduction to overfitting in regression-type models. Psychosomatic Medicine 66(3):411–421.

Ballance, L. T., R. L. Pitman, and P. C. Fiedler. 2006. Oceanographic influences on seabirds and cetaceans of the eastern tropical Pacific: A review. Progress in Oceanography 69(2-4):360-390.

Bamburak, J. D. and Nicolas, M. P. B. 2010: Gammon Ferruginous Member of the Cretaceous Pierre Shale in southwestern Manitoba: distribution and mineral potential (parts of NTS 62F, G, J, K, N, O, 63C); pp. 170–177 in Report of Activities 2010. Manitoba Innovation, Energy and Mines, and the Manitoba Geological Survey, Winnipeg, Manitoba, Canada. Report GS-15.

Barbet-Massin, M., F. Jiguet, C. H. Albert, and W. Thuiller. 2012. Selecting pseudo-absences for species distribution models: how, where and how many? Methods in Ecology and Evolution 3(2):327-338.

Bardack, D. 1968. Fossil vertebrates from the marine Cretaceous of Manitoba. Canadian Journal of Earth Sciences 5(1):145-153.

Bell, G. L., Jr. 1997. A phylogenetic revision of North American and Adriatic Mosasauroidea; pp. 293-332 *in* Callaway, J.M., and Nicholls, E.L. (eds.), Ancient Marine Reptiles. Academic Press, San Diego, California.

Bell, G. L., Jr., and K. R. Barnes. 2007. First record of stomach contents in *Tylosaurus nepaeolicus* and comments on predation among Mosasauridae; pp. 6-7 in M. J. Everhart (ed.), Second Mosasaur Meeting Abstract Booklet and Field Guide, Sternberg Museum of Natural History, Hays, Kansas, 2-6 May 2007.

Bell, A., and L. M. Chiappe. 2015. Identification of a new hesperornithiform from the Cretaceous Niobrara Chalk and implications for ecologic diversity among early diving birds. PLoS ONE 10(11; e0141690):34 pp.

Bell, A., and L. M. Chiappe. 2016. A species-level phylogeny of the Cretaceous Hesperornithiformes (Aves: Ornithuromorpha): implications for body size evolution amongst the earliest diving birds. Journal of Systematic Palaeontology 14(3):239-251.

Bell, A., K. J. Irwin, and L. C. Davis. 2015. Hesperornithiform birds from the Late Cretaceous (Campanian) of Arkansas, USA. Transactions of the Kansas Academy of Science 118(3/4):219-229.

Bell, A., Y.-H. Wu, and L. M. Chiappe. 2019. Morphometric comparison of the Hesperornithiformes and modern diving birds. Palaeogeography, Palaeoclimatology, Palaeoecology 513:196-207.

Bell, P. R., F. Fanti, M. T. Mitchell, and P. J. Currie. 2014. Marine reptiles (Plesiosauria and Mosasauridae) from the Puskwaskau Formation (Santonian–Campanian), west-central Alberta. Journal of Paleontology 88(1):187-194.

Benton, M. J. 1996a. Testing the roles of competition and expansion in tetrapod evolution. Proceedings of the Royal Society of London B: Biological Sciences 263(1370):641–646.

Benton, M. J. 1996b. On the nonprevalence of competitive replacement in the evolution of tetrapods; pp. 185–210 (Chapter 8) in D. Jablonski, D. H. Erwin, and J. H. Lipps (eds.), Evolutionary Paleobiology. University of Chicago Press, Chicago.

Benton, M. Ruta, A. M. Dunhill, and M. Sakamoto. 2013. The first half of tetrapod evolution, sampling proxies, and fossil record quality. Palaeogeography, Palaeoclimatology, Palaeoecology 372:18-41.

Bigg, G. R., C. W. Cunningham, G. Ottersen, G. H. Pogson, M. R. Wadley, and P. Williamson. 2008. Ice-age survival of Atlantic cod: agreement between palaeoecology models and genetics. Proceedings of the Royal Society B: Biological Sciences 275:163-172.

Blakey, R. C. 2014. Paleogeography and paleotectonics of the Western Interior Seaway, Jurassic-Cretaceous of North America. American Association of Petroleum Geologists, Search and Discovery Article 30392:72 pp.

Boersma, P. D., G. A. Rebstock, E. Frere, and S. E. Moore. 2009. Following the fish: penguins and productivity in the South Atlantic. Ecological Monographs 79(1):59-76.

Booth, T. H., H. A. Nix, J. R. Busby, and M. F. Hutchinson. 2014. BIOCLIM: the first species distribution modelling package, its early applications and relevance to most current MaxEnt studies. Diversity and Distributions 20(1):1-9.

Boyle, T. P., G. M. Smillie, J. C. Anderson, and D. R. Beeson. 1990. A sensitivity analysis of nine diversity and seven similarity indices. Research Journal of the Water Pollution Control Federation 62(6):749-762.

Brame, H.-M. R., and A. L. Stigall. 2014. Controls on niche stability in geologic time: congruent responses to biotic and abiotic environmental changes among Cincinnatian (Late Ordovician) marine invertebrates. Paleobiology 40(1):70–90.

Brinkman, D. B. 1990. Paleoecology of the Judith River Formation (Campanian) of Dinosaur Provincial Park, Alberta, Canada: Evidence from vertebrate microfossil localities. Palaeogeography, Palaeoclimatology, Palaeoecology 78:37-54.

Brinkman, D. B., D. R. Braman, A. G. Neuman, P. E. Ralrick, and T. Sato. 2005. A vertebrate assemblage from the marine shales of the Lethbridge Coal Zone; pp. 486-500 of P. J. Currie and E. B. Koppelhus (eds.), Dinosaur Provincial Park: A spectacular ancient ecosystem revealed. Indiana University Press, Bloomington and Indianapolis, Indiana.

Bryant. L. J. 1983. *Hesperornis* in Alaska. Paleobios 40:1-8.

Bullard, T. S., and M. W. Caldwell. 2010. Redescription and rediagnosis of the tylosaurine mosasaur *Hainosaurus pembinensis* Nicholls, 1988, as *Tylosaurus pembinensis* (Nicholls, 1988). Journal of Vertebrate Paleontology 30(2):416-426.

Burnham, K. P., and D. R. Anderson. 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach (Second edition). Springer-Verlag New York, Inc., New York, New York, 488 pp.

Burnham, K. P., D. R. Anderson, and K. P. Huyvaert. 2011. AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. Behavioral Ecology and Sociobiology 65:23-35.

Busby, J. R. 1991. BIOCLIM - A bioclimate analysis and prediction system; pp. 64-68 in C. R. Margules and M. P. Austin (eds.), Nature conservation: cost effective biological surveys and data analysis. CSIRO, Melbourne, Australia. Proceedings of the Cost Effective Biological Surveys and Data Analysis Workshop, Sydney, Australia, March 1988.

Campbell, J. A., M. T. Mitchell, M. J. Ryan, and J. S. Anderson. 2021. A new elasmosaurid (Sauropterygia: Plesiosauria) from the non-marine to paralic Dinosaur Park Formation of southern Alberta, Canada. PeerJ 9(e10720):44 pp.

Canty, A., and B. Ripley (2020). boot: Bootstrap R (S-Plus) functions. R package version 1.3-25. Available at https://cran.r-project.org/web/packages/boot/index.html.

Carotenuto, F., M. Di Febbraro, A. Mondanaro, S. Castiglione, C. Serio, M. Melchionna, L. Rook, and P. Raia. 2020. MInOSSE: A new method to reconstruct geographic ranges of fossil species. Methods in Ecology and Evolution 11(9):1121-1132.

Carpenter, K. 1999. Revision of North American elasmosaurs from the Cretaceous of the Western Interior. Paludicola 2(2):148-173.

Carpenter, K. 2006. Comparative vertebrate taphonomy of the Pembina and Sharon Springs Members (middle Campanian) of the Pierre Shale, Western Interior. Paludicola 5(4):125-149.

Carrier, A. E. 2018. Investigation of molluscan survivorship across the Cenomanian-Turonian Boundary Event using ecological niche modeling. M.S. thesis, The University of New Mexico, Albuquerque, New Mexico, 144 pp.

Carrier, A., and C. Myers. 2018. Testing niche stability in Western Interior Seaway cephalopods and other mollusks across the environmental perturbation of OAE2. Geological Society of America Abstracts with Programs 50(6):163-4.

Carrino, M. H. 2007. Taxonomic comparison and stratigraphic distribution of *Toxochelys* (Testudines: Cheloniidae) of South Dakota; pp. 111-132 in J. E. Martin, and D. C. Parris (eds.), The Geology and Paleontology of the Late Cretaceous Marine Deposits of the Dakotas. The Geological Society of America, Boulder, Colorado. The Geological Society of America Special Paper 427.

Case, G. R. 1987. A new selachian fauna from the late Campanian of Wyoming (Teapot Sandstone Member, Mesaverde Formation, Big Horn Basin). Palaeontographcia. Abteilung A Band A197(Lieferung 1-3):1-37.

Cavin, L., A. Alexopoulous, and A. Piuz. 2012. Late Cretaceous (Maastrichtian) ray-finned fishes from the island of Gavdos, southern Greece, with comments on the evolutionary history of the aulopiform teleost *Enchodus*. Bulletin de la Société Géologique de France 183(6):561-572.

Chambert, T., D. A. W. Miller, and J. D. Nichols. 2015. Modeling false positive detections in species occurrence data under different study designs. Ecology 96(2):332-339.

Chessel, D., A. B. Dufour, and J. Thioulouse. 2004. The ade4 package - I: One-table methods. R News 4(1):5-10.

Chin, K., J. Bloch, A. Sweet, J. Tweet, J. Eberle, S. Cumbaa, J. Witkowski, and D. Harwood. 2008. Life in a temperate polar sea: A unique taphonomic window on the structure of a Late Cretaceous Arctic marine ecosystem. Proceedings of the Royal Society B: Biological Sciences 275(1652):2675-2685.

Christiansen, P., and N. Bonde. 2002. A new species of gigantic mosasaur from the Late Cretaceous of Israel. Journal of Vertebrate Paleontology 22(3):629-644.

Cicimurri, D. J., and M. J. Everhart. 2001. An elasmosaur with stomach contents and gastroliths from the Pierre Shale (Late Cretaceous) of Kansas. Transactions of the Kansas Academy of Science 104(3-4):129-143.

Cohen, K. M., S. C., Finney, P. L. Gibbard, and J.-X. Fan. 2013; updated. The ICS International Chronostratigraphic Chart 2021/07. Episodes 36(3):199-204.

Compagno, L. J. V. 2001. Bullhead, mackerel and carpet sharks (Heterodontiformes, Lamniformes, and Orectolobiformes); in Sharks of the World: An annotated and illustrated catalogue of shark species known to date, Volume 2. FAO Species Catalogue for Fishery Purposes No. 1, Vol. 2. Food and Agriculture Organization of the United Nations, Rome, Italy, 269 pp.

Crampton, J. S., A. G. Beu, R. A. Cooper, C. M. Jones, B. Marshall, and P. A. Maxwell. 2003. Estimating the rock volume bias in paleobiodiversity studies. Science 301(5631):358-360.

Dalgaard, P. 2008. Introductory Statistics with R, Second Edition. Springer Science+Business Media, LLC, New York, New York, 363 pp.

Dambach, J., and D. Rödder. 2011. Applications and future challenges in marine species distribution modeling. Aquatic Conservation: Marine and Freshwater Ecosystems 21(1):92-100.

Davison, A. C., and D. V. Hinkley (eds.). 1997. Bootstrap Methods and Their Application. Cambridge University Press, Cambridge, United Kingdom, 594 pp.

DeMar, Jr., D. G., and B. H. Breithaupt. 2008. Terrestrial and aquatic vertebrate paleocommunities of the Mesaverde Formation (Upper Cretaceous, Campanian) of the Wind River and Bighorn Basins, Wyoming, USA: pp. 78-103 in J. T. Sankey and S. Baszio (eds.), Vertebrate Microfossil Assemblages: Their Role in Paleoecology and Paleobiogeography. Life of the Past series. Indiana University Press, Bloomington, Indiana, 296 pp.

Dennis, K. J., J. K. Cochran, N. H. Landman, and D. P. Schrag. 2013. The climate of the Late Cretaceous: New insights from the application of the carbonate clumped isotope thermometer to Western Interior Seaway macrofossil. Earth and Planetary Science Letters 362:51-65.

Dicken, M. L., N. E. Hussey, H. M. Christiansen, M. J. Smale, N. Nkabi, G. Cliff, and S. P. Wintner. 2017. Diet and trophic ecology of the tiger shark (*Galeocerdo cuvier*) from South African waters. PLoS ONE 12(6:e0177897):25 pp.

Dobson, A. J., and A. G. Barnett. 2008. An Introduction to Generalized Linear Models (Third Edition); in B. P. Carlin, J. J. Faraway, M. Tanner, and J. Zidek (eds.), Chapman & Hall/CRC Texts in Statistical Science Series. CRC Press LLC, Boca Raton, Florida, 320 pp.

Dorazio, R. M. 2014. Accounting for imperfect detection and survey bias in statistical analysis of presence-only data. Global Ecology and Biogeography 23(12):1472-1484.

Dray, S., and A.-B. Dufour. 2007. The ade4 Package: Implementing the duality diagram for ecologists. Journal of Statistical Software 22(4):20 pp.

Dray, S., A. B. Dufour, and D. Chessel. 2007. The ade4 Package — II: Two-table and K-table methods. R News 7(2):47-52.

Druckenmiller, P. S., A. J. Daun, J. L. Skulan, and J. C. Pladziewicz. 1993. Stomach contents in the Upper Cretaceous shark *Squalicorax falcatus*. Journal of Vertebrate Paleontology 13(3, Supplement):33A-34A.

Dudei, N. L., and A. L. Stigall. 2010. Using ecological niche modeling to assess biogeographic and niche response of brachiopod species to the Richmondian Invasion (Late Ordovician) in the Cincinnati Arch. Palaeogeography, Palaeoclimatology, Palaeoecology 296(1-2):28-43.

Dumont, M., P. Tafforeau, T. Bertin, B.-A. Bhullar, D. Field, A. Schulp, B. Strilisky, B. Thivichon-Prince, L. Viriot, and A. Louchart. 2016. Synchrotron imaging of dentition provides insights into the biology of *Hesperornis* and *Ichthyornis*, the “last” toothed birds. BMC Evolutionary Biology 16(178):28 pp.

Dunhill, A. M. 2011. Using remote sensing and a geographic information system to quantify rock exposure area in England and Wales: Implications for paleodiversity studies. Geology 39(2):111-114.

Dunhill, A. M. 2012. Problems with using rock outcrop area as a paleontological sampling proxy: rock outcrop and exposure area compared with coastal proximity, topography, land use, and lithology. Paleobiology 38(1):126-143.

Dunhill, A. M., M. J. Benton, R. J. Twitchett, and A. J. Newell. 2012. Completeness of the fossil record and the validity of sampling proxies at outcrop level. Palaeontology 55(6):1155-1175.

Dutchak, A. R., and M. W. Caldwell. 2009. A redescription of *Aigialosaurus* (= *Opetiosaurus*) *bucchichi* (Kornhuber, 1901) (Squamata: Aigialosauridae) with comments on mosasauroid systematics. Journal of Vertebrate Paleontology 29(2):437-452.

Dutel, H., J. G. Maisey, D. R. Schwimmer, P. Janvier, M. Herbin, and G. Clément. 2012. The giant cretaceous coelacanth (Actinistia, Sarcopterygii) *Megalocoelacanthus dobiei* Schwimmer, Stewart & Williams, 1994, and its bearing on Latimerioidei interrelationships. PLoS ONE 7(11; e49911):27 pp.

Eaton, J. G., R. L. Cifelli, J. H. Hutchison, J. I. Kirkland, and J. M. Parrish. 1999. Cretaceous vertebrate faunas from the Kaiparowits Plateau, south-central Utah; pp. 345-353 in D. D. Gillette (ed.), Vertebrate Paleontology in Utah. Utah Geological Survey, Miscellaneous Publication 99-1.

Ehret, D. J., and T. L. Harrell. 2018. Feeding traces on a *Pteranodon* (Reptilia: Pterosauria) bone from the Late Cretaceous (Campanian) Mooreville Chalk in Alabama, USA. PALAIOS 33(9):414-418.

Elderbak, K., and R. M. Leckie. 2016. Paleocirculation and foraminiferal assemblages of the Cenomanian-Turonian Bridge Creek Limestone bedding couplets: Productivity vs. dilution during OAE2. Cretaceous Research 60:52-77.

Elith, J., and J. Franklin. 2013. Species distribution modeling; pp. 692-705 in S. Levin (ed.), Encyclopedia of Biodiversity, 2nd Edition, Volume 6. Academic Press, 5504 pp.

Elith, J., and J. R. Leathwick. 2009. Species distribution models: Ecological explanation and prediction across space and time. Annual Review of Ecology, Evolution, and Systematics 40:677-697.

Elith, J., S. J. Phillips, T. Hastie, M. Dudík, Y. E. Chee, and C. J. Yates. 2011. A statistical explanation of MaxEnt for ecologists. Diversity and Distributions 17(1):43-57.

Elith, J., C. H. Graham, R. P. Anderson, M. Dudík, S. Ferrier, A. Guisan, R. J. Hijmans, F. Huettmann, J. R. Leathwick, A. Lehmann, J. Li, L. G. Lohmann, B. A. Loiselle, G. Manion, C. Moritz, M. Nakamura, Y. Nakazawa, J. McC. Overton, A. T. Peterson, S. J. Phillips, K. Richardson, R. Scachetti-Pereira, R. E. Schapire, J. Soberón, S. Williams, M. S. Wisz, and N. E. Zimmermann. 2006. Novel methods improve prediction of species' distributions from occurrence data. Ecography 29(2):129-151.

Elzanowski, A. 1983. Birds in Cretaceous ecosystems; pp. 75-93 in the Second Symposium on Mesozoic Terrestrial Ecosystems, Jadwisin, Poland, 1981. Acta Palaeontologica Polonica 28(1-2).

ESRI, Inc. 2019. ArcMap 10.7.1. Available at https://desktop.arcgis.com/en/arcmap/.

ESRI, Inc. 2020. ArcGIS Online. Available at https://www.esri.com/en-us/arcgis/products/arcgis-online/overview.

ESRI, Inc. 2021. ArcGIS Pro 2.9.0. Available at https://www.esri.com/en-us/arcgis/products/arcgis-pro/overview.

Etz, A. 2018. Introduction to the concept of likelihood and its applications. Advances in Methods and Practices in Psychological Science 1(1):60-69.

Everhart, M. J. 2004a. Plesiosaurs as the food of mosasaurs; new data on the stomach contents of *Tylosaurus proriger* (Squamata; Mosasauridae) from the Niobrara Formation of Western Kansas. The Mosasaur 7:41-46.

Everhart, M. J. 2004b. Late Cretaceous interaction between predators and prey. Evidence of feeding by two species of shark on a mosasaur. PalArch Journal of Vertebrate Palaentology 1(1):7 pp.

Everhart, M. J., A. Maltese, and J. Jett. 2013. Mosasaur predation on turtles in the Smoky Hill Chalk of western Kansas; pp. 16-17 in M. J. Polcyn and L. L. Jacobs (eds.), 4th Triennial International Mosasaur Meeting Program and Abstracts, Southern Methodist University, Dallas, Texas, 20-25 May 2013.

Everhart, M. J. 2017. Oceans of Kansas: A Natural History of the Western Interior Sea, Second Edition. Indiana University Press, Bloomington, Indiana, 460 pp.

Fauchald, P. 2009. Spatial interaction between seabirds and prey: review and synthesis. Marine Ecology Progress Series 391:139-151.

Feduccia, A. 1999. The Cretaceous – Divers and Seabirds, Old and New; pp. 139-194 in A. Feduccia (ed.), The Origin and Evolution of Birds, Second Edition. Yale University Press, New Haven and London, 480 pp.

Fenton, M. M., E. J. Waters, S. M. Pawley, N., Atkinson, D. J. Utting, and K. Mckay. 2013. Surficial geology of Alberta, Canada. 1:000000. Alberta Energy Regulator/Alberta Geological Survey Map 601. Available at https://ags.aer.ca/publication/map-601.

Feranec, R. S., E. A. Hadly, and A. Paytan. 2009. Stable isotopes reveal seasonal competition for resources between late Pleistocene bison (*Bison*) and horse (*Equus*) from Rancho La Brea, southern California. Palaeogeography, Palaeoclimatology, Palaeoecology 271(1-2):153–160.

Fisher, C. G., and W. W. Hay. 1999. Calcareous nannofossils as indicators of mid-Cretaceous paleofertility along an ocean front, U. S. Western Interior. Geological Society of America Special Papers 332:161-180.

Fox, R. C. 1974. A middle Campanian, nonmarine occurrence of the Cretaceous toothed bird *Hesperornis* Marsh. Canadian Journal of Earth Sciences 11(9):1335-1338.

Gelfand, A. E., and S. Shirota. 2019. Preferential sampling for presence/absence data and for fusion of presence/absence data with presence-only data. Ecological Monographs, 89(3; e01372):17 pp.

Gentry, A. D., and J. A. Ebersole. 2018. The first report of *Toxochelys latiremis* Cope, 1873 (Testudines: Panchelonioidea) from the early Campanian of Alabama, USA. Paleobios 35:10 pp.

Gill, J. R., and W. A. Cobban. 1966. The Red Bird Section of the Upper Cretaceous Pierre Shale in Wyoming; pp. A1-73 in Stratigraphy, Paleontology, and Sedimentation of a Classic Reference Locality of the Pierre Shale. United States Government Printing Office, Washington, D.C. U.S. Geological Survey Professional Paper 393-A.

Google, LLC. 2020. Google Earth Pro 7.3.3.7786. Available at https://www.google.com/earth/versions/.

Goody, P. C. 1976. *Enchodus* (Teleostei: Enchodontidae) from the Upper Cretaceous Pierre Shale of Wyoming and South Dakota with an evaluation of the North American enchodontid species. Palaeontographica Abteilung A: Paläozoologie-Stratigraphie 152(4-6):91-112.

Guillera-Arroita, G., J. J. Lahoz-Monfort, J. Elith, A. Gordon, H. Kujala, P. E. Lentini, M. A. McCarthy, R. Tingley, and B. A. Wintle. 2015. Is my species distribution model fit for purpose? Matching data and models to applications. Global Ecology and Biogeography 24(3):276-292.

Guisan, A., T. C. Edwards, and T. Hastie. 2002. Generalized linear and generalized additive models in studies of species distributions: setting the scene. Ecological Modelling 157(2-3):89-100.

Hanczaryk, P. A., and W. B. Gallagher. 2007. Stratigraphy and paleoecology of the middle Pierre Shale along the Missouri River, central South Dakota; pp. 51-69 in

James E. Martin and David C. Parris (eds.), The Geology and Paleontology of the Late Cretaceous Marine Deposits of the Dakotas. The Geological Society of America, Boulder, Colorado. The Geological Society of America Special Paper 427.

Hanks, H., and K. Shimada. 2002. Vertebrate fossils, including non-avian dinosaur remains and the first shark-bitten bird bone, from a Late Cretaceous (Turonian) marine deposit of northeastern South Dakota. Journal of Vertebrate Paleontology 22(3, Supplement):62A.

Harrell, Jr., T. L., and D. J. Ehret. 2019. Lungfish tooth plates (Sarcopterygii, Dipnoi) from the Late Cretaceous (Santonian) Eutaw Formation of Alabama and Mississippi, USA. Journal of Paleontology 93(3):531-542.

Hastie, T., R. Tibshirani, and J. Friedman. 2009. The Elements of Statistical Learning: Data Mining, Inference, and Prediction, Second Edition; in P. Bickel, P. Diggle, S. Fienberg, U. Gather, I. Olkin, and S. Zeger (advisors), Springer Series in Statistics. Springer Science+Business Media, LLC, New York, New York, 745 pp.

Haq, B. U., J. Hardenbol, and P. R. Vail. 1987. Chronology of fluctuating sea levels since the Triassic. Science 235(4793):1156-1167.

He, S., T. K. Kyser, and W. G. E. Caldwell. 2005. Paleoenvironment of the Western Interior Seaway inferred from $\delta^{18}O$ and $\delta^{13}C$ values of molluscs from the Cretaceous Bearpaw marine cyclothem. Palaeogeography, Palaeoclimatology, Palaeoecology 217(1-2):67-85.

Hedgren, S., and Å. Linnman. 1979. Growth of guillemot *Uria aalge* chicks in relation to time of hatching. Ornis Scandinavica 10(1):29-36.

Heumann, C., and M. S. Shalabh. 2016. Introduction to Statistics and Data Analysis. Springer International Publishing Switzerland, Cham, Switzerland, 456 pp.

Hills, L. V., E.L. Nicholls, L. (K.) M. Núñez-Betelu, and D.J. McIntyre. 1999. *Hesperornis* (Aves) from Ellesmere Island and palynological correlation of known Canadian localities. Canadian Journal of Earth Sciences 36(9):1583-1588.

Hines, J. E. 2006. PRESENCE- Software to estimate patch occupancy and related parameters. USGS-PWRC, Laurel, Maryland, United States. Available at: http://www.mbr-pwrc.usgs.gov/software/presence.html.

Hoganson, J. W., M. Hanson, D. L. Halvorson, and V. Halvorson. 1996. Mosasaurs, sharks, and other marine creatures from the Cooperstown Pierre Shale Site. NDGS Newsletter 23(2-3):20-26.

Irmis, R. B., J. H. Whiteside, and C. F. Kammerer. 2013. Non-biotic controls of observed diversity in the paleontologic record: An example from the Permo-Triassic Karoo Basin of South Africa. Palaeogeography, Palaeoclimatology, Palaeoecology 372:62-77.

James, G. Daniela Witten, Trevor Hastie, and Robert Tibshirani. 2013. An Introduction to Statistical Learning with Applications in R; in G. Casella, S. Fienberg, and I. Olkin (eds.), Springer Texts in Statistics. Springer Science+Business Media, LLC, New York, New York, 426 pp.

Janzic, A.-M. 2006. A preliminary analysis of stomach contents from a new polycotylid plesiosaur. Journal of Vertebrate Paleontology 26(3, Supplement):81A

Jones, T., J. K. Parrish, W. T. Peterson, E. P. Bjorkstedt, N. A. Bond, L. T. Ballance, V. Bowes, J. M. Hipfner, H. K. Burgess, J. E. Dolliver, K. Lindquist, J. Lindsey, H. M. Nevins, R. R. Robertson, J. Roletto, L. Wilson, T. Joyce, and J. Harvey. 2018. Massive mortality of a planktivorous seabird in response to a marine heatwave. Geophysical Research Letters 45(7):3193-3202.

Kass, M. S. 1999. *Prognathodon stadtmani*: (Mosasauridae) A new species from the Mancos Shale (lower Campanian) of western Colorado; pp. 275-294 in D. D. Gillette (ed.), Vertebrate Paleontology in Utah. Utah Geological Survey, Miscellaneous Publication 99-1.

Kear, B. P., D. Larsson, J. Lindgren, and M. Kundrát. 2017. Exceptionally prolonged tooth formation in elasmosaurid plesiosaurians. PLoS ONE 12(2:e0172759):14 pp.

Koshkina, V., Y. Wang, A. Gordon, R. M. Dorazio, M. White, and Lewi Stone. 2017. Integrated species distribution models: combining presence-background data and site-occupancy data with imperfect detection. Methods in Ecology and Evolution 8(4):420-430.

Kubo, T., M. T. Mitchell, and D. M. Henderson. 2012. *Albertonectes vanderveldei,* a new elasmosaur (Reptilia, Sauropterygia) from the Upper Cretaceous of Alberta. Journal of Vertebrate Paleontology 32(3):557-572.

Lahoz-Monfort, J. J., G. Guillera-Arroita, and B. A. Wintle. 2014. Imperfect detection impacts the performance of species distribution models. Global Ecology and Biogeography 23(4):504-515.

Landman, N. H., J. K. Cochran, M. Slovacek, N. L. Larson, M. P. Garb, J. Brezina, and J. D. Witts. 2018. Isotope sclerochronology of ammonites (*Baculites compressus*) from methane seep and non-seep sites in the Late Cretaceous Western Interior Seaway, USA: Implications for ammonite habitat and mode of life. American Journal of Science 318(6):603-639.

Lawing, A. M., J. L. Blois, K. C. Maguire, S. J. Goring, Y. Wang, and J. L. McGuire. 2021. Occupancy models reveal regional differences in detectability and improve relative abundance estimations in fossil pollen assemblages. Quaternary Science Reviews 253(106747):13 pp.

Lele, S. R., J. L. Keim, and P. Solymos. 2019. ResourceSelection: Resource selection (probability) functions for use-availability data. R package version 0.3-5. Available at https://CRAN.R-project.org/package=ResourceSelection.

Lillegraven, J. A., and M. C. McKenna. 1986. Fossil mammals from the "Mesaverde" Formation (Late Cretaceous, Judithian) of the Bighorn and Wind River Basins, Wyoming, with definitions of Late Cretaceous North American Land-Mammal "Ages". American Museum Novitates 2840:68 pp.

Liow, L. H. 2013. Simultaneous estimation of occupancy and detection probabilities: an illustration using Cincinnatian brachiopods. Paleobiology 39(2):193-213.

Lively, J. R. 2018. Taxonomy and historical inertia: *Clidastes* (Squamata: Mosasauridae) as a case study of problematic paleobiological taxonomy. A global perspective on Mesozoic marine reptiles, Proceedings of the 5th Triennial Mosasaur Meeting, Uppsala, Sweden, 16-20 May 2016. Alcheringa: An Australasian Journal of Palaeontology 42(4):516–527.

Locklair, R. E., and B. B. Sageman. 2008. Cyclostratigraphy of the Upper Cretaceous Niobrara Formation, Western Interior, U.S.A.: A Coniacian–Santonian orbital timescale. Earth and Planetary Science Letters 269(3-4):540-553.

Lockshin, S. N., M. M. Yacobucci, P. Gorsevski, and A. Gregory. 2017. Spatial characterization of Cretaceous Western Interior Seaway paleoceanography using foraminifera, fuzzy sets and Dempster–Shafer theory. GeoResJ 14:98-120.

Long J. A. 2020. jtools: Analysis and presentation of social scientific data. R package version 2.1.0. Available at https://cran.r-project.org/package=jtools.

Long, R. A., Therese M. Donovan, Paula MacKay, William J. Zielinski, and Jeffrey S. Buzas. 2011. Predicting carnivore occurrence with noninvasive surveys and occupancy modeling. Landscape Ecology 26:327-340.

Longman, M. W., B. A. Luneau, and S. M. Landon. 1998. Nature and distribution of Niobrara lithologies in the Cretaceous Western Interior Seaway of the Rocky Mountain region. The Mountain Geologist 35(4):137-170.

Lowe, C. G., B. M. Wetherbee, G. L. Crow, and A. L. Tester. 1996. Ontogenetic dietary shifts and feeding behavior of the tiger shark, *Galeocerdo cuvier*, in Hawaiian waters. Environmental Biology of Fishes 47:203-211.

Lowery, C. M., R. M. Leckie, R. Bryant, K. Elderbak, A. Parker, D. E. Polyak, M. Schmidt, O. Snoeyenbos-West, and Erica Sterzinar. 2018. The Late Cretaceous Western Interior Seaway as a model for oxygenation change in epicontinental restricted basins. Earth-Science Reviews 177:545-564.

MacKenzie, D. I., J. D. Nichols, G. B. Lachman, S. Droege, J. A. Royle, and C. A. Langtimm. 2002. Estimating site occupancy rates when detection probabilities are less than one. Ecology 83(8):2248-2255.

MacKenzie, D. I., J. D. Nichols, J. A. Royle, K. H. Pollock, L. L. Bailey, and J. E. Hines. 2018. Occupancy Estimation and Modeling: Inferring Patterns and Dynamics of Species Occurrence (Second Edition). Academic Press, Elsevier, San Diego, California, 648 pp.

Madzia, D. and A. Cau. 2020. Estimating the evolutionary rates in mosasauroids and plesiosaurs: discussion of niche occupation in Late Cretaceous seas. PeerJ 8(e8941):31 pp.

Maguire, K. C., and A. L. Stigall. 2008. Paleobiogeography of Miocene Equinae of North America: a phylogenetic biogeographic analysis of the relative roles of climate, vicariance, and dispersal. Palaeogeography, Palaeoclimatology, Palaeoecology 267(3-4):175-184.

Maguire, K. C., and A. L. Stigall. 2009. Using ecological niche modeling for quantitative biogeographic analysis: a case study of Miocene and Pliocene Equinae in the Great Plains. Paleobiology 35(4):587–611.

Malizia, R. W., and A. L. Stigall. 2011. Niche stability in Late Ordovician articulated brachiopod species before, during, and after the Richmondian Invasion. Palaeogeography, Palaeoclimatology, Palaeoecology 311(3-4):154-170.

Marenco, K. N., and J. W. Hagadorn. 2019. Big bedding planes: Outcrop size and spatial heterogeneity influence trace fossil analyses. Palaeogeography, Palaeoclimatology, Palaeoecology 513:14-24.

Marks, M. A., R. K. Brooke, and A. M. Gildenhuys. 1997. Cape fur seal *Arctocephalus pusillus* predation on cape cormorants *Phalacrocorax capensis* and other birds at Dyer Island, South Africa. Marine Ornithology 25:9-12.

Martin, J. E, and P. R. Bjork. 1987. Gastric residues associated with a mosasaur from the Late Cretaceous (Campanian) Pierre Shale in South Dakota; pp. 68-72 in J. E. Martin and G. E. Ostrander (eds.), Papers in Paleontology in Honor of Morton Green, South Dakota School of Mines and Technology, Museum of Geology. Dakoterra 3.

Martin, J. E., B. A. Schumacher, D. C. Parris, and B. S. Grandstaff. 1998. Fossil vertebrates of the Niobrara Formation in South Dakota; pp. 39-54 in J. E. Martin, J. W. Hoganson, and R. C. Benton (eds.), Proceedings for the Fifth Conference on Fossil Resources – Partners Preserving Our Past, Planning Our Future, Badlands National Park and the Museum of Geology at the South Dakota School of Mines and Technology. Dakoterra 5, Museum of Geology at the South Dakota School of Mines and Technology.

Martin, L. D., and J.-D. Lim. 2002. New information on the hesperornithiform radiation; pp. 165-174 in Z. Zhou and F. Zhang (eds.), Proceedings of the 5th Symposium of the Society of Avian Paleontology and Evolution, Beijing, China, 1-4 June 2000.

Martin, L. D., and J. Tate., Jr. 1967. A *Hesperornis* from the Pierre Shale; pp. 40 in Proceedings of the Annual Meeting of the Nebraska Academy of Sciences and Affiliated Societies 77.

Martin, L. D., and J. Tate., Jr. 1976. The skeleton of *Baptornis advenus* (Aves: Hesperornithiformes); pp. 35-66 in S. L. Olson (ed.), Collected Papers in Avian

Paleontology Honoring the 90th Birthday of Alexander Whitmore, Smithsonian Institution Press, Washington, D.C. Smithsonian Contributions to Paleobiology 27.

Martin, L. D., B. M. Rothschild, and D. A. Burnham. 2016. *Hesperornis* escapes plesiosaur attack. Cretaceous Research 63:23-27.

Massare, J. A. 1987. Tooth morphology and prey preference of Mesozoic marine reptiles. Journal of Vertebrate Paleontology 7(2):121-137.

Matović, N., B. Cadiou, D. Oro, and A. Sanz-Aguilar. 2017. Disentangling the effects of predation and oceanographic fluctuations in the mortality of two allopatric seabird populations. Population Ecology 59:225-238.

McFadden, D. 1974. Conditional logit analysis of qualitative choice behavior; pp. 105-142 in P. Zarembka (ed.), Frontiers in Econometrics (Chapter 4). Academic Press, New York, New York.

McHenry, C. R., A. G. Cook, and S. Wroe. 2005. Bottom-feeding plesiosaurs. Science 310(5745):75.

Melchionna, M., M. Di Febbraro, F. Carotenuto, L. Rook, A. Mondanaro, S. Castiglione, C. Serioa, V. A. Veroa, G. Tesone, M. Piccolo, J. A. F. Diniz-Filho, and P. Raia. 2018. Fragmentation of Neanderthals' pre-extinction distribution by climate change. Palaeogeography, Palaeoclimatology, Palaeoecology 496:146-154.

Melo-Merino, S. M., H. Reyes-Bonilla, and A. Lira-Noriega. 2020. Ecological niche models and species distribution models in marine environments: A literature review and spatial analysis of evidence. Ecological Modelling 415(108837):35 pp.

Menke, S. B., D. A. Holway, R. N. Fisher, and W. Jetz. 2009. Characterizing and predicting species distributions across environments and scales: Argentine ant occurrences in the eye of the beholder. Global Ecology and Biogeography 18(1):50-63.

Meyer, R. L. 1974. Late Cretaceous elasmobranchs from the Mississippi and east Texas embayments of the Gulf Coastal Plain. Ph.D. dissertation, Southern Methodist University, Dallas, Texas, 419 pp.

Meyer, C. G., Y. P. Papastamatiou, and K. N. Holland. 2010. A multiple instrument approach to quantifying the movement patterns and habitat use of tiger (*Galeocerdo cuvier*) and Galapagos sharks (*Carcharhinus galapagensis*) at French Frigate Shoals, Hawaii. Marine Biology 157:1857-1868.

Müller, R. D., M. Sdrolias, C. Gaina, B. Steinberger, and C. Heine. 2008. Long-term sea-level fluctuations driven by ocean basin dynamics. Science 319:1357-1362.

Müller, R. D., J. Cannon, X. Qin, R. J. Watson, M. Gurnis, S. Williams, T. Pfaffelmoser, M. Seton, S. H. J. Russell, and S. Zahirovic. 2018. GPlates: building a virtual Earth through deep time. Geochemistry, Geophysics, Geosystems 19(7):2243-2261.

Myers, C. E., and B. S. Lieberman. 2011. Sharks that pass in the night: Using geographical information systems to investigate competition in the Cretaceous Western Interior Seaway. Proceedings of the Royal Society of London B 278(1706):681–689.

Myers, C. E., R. A. MacKenzie III, and B. S. Lieberman. 2013. Greenhouse biogeography: the relationship of geographic range to invasion and extinction in the Cretaceous Western Interior Seaway. Paleobiology 39(1):135-148

Myers, C. E., A. L. Stigall, and B. S. Lieberman. 2015. PaleoENM: applying ecological niche modeling to the fossil record. Paleobiology 41(2):226-244.

Neumann, C. 2000. Evidence of predation on Cretaceous sea stars from northwest Germany. Lethaia 33:65-70.

Nicholls, E. L., and A. P. Russell. 1990. Paleobiogeograhy of the Cretaceous Western Interior Seaway of North America: the vertebrate evidence. Palaeogeography, Palaeoclimatology, Palaeoecology 79(1-2):149-169.

Nix, H. 1986. A biogeographic analysis of Australian elapid snakes; pp. 4-15 in R. Longmore (ed.), Snakes: Atlas of Elapid Snakes of Australia. Australian Government Publishing Service, Canberra, Australia. Bureau of Flora and Fauna, Canberra, Australian Flora and Fauna Series 7.

Ogg, J. G., and L. A. Hinnov. 2012. Chapter 27-Cretaceous; pp. 793-853 in F. M. Gradstein, J. G. Ogg, M. D. Schmitz, and G. M. Ogg (eds.), The Geologic Time Scale 2012, v. 2. Elsevier, Amsterdam, The Netherlands.

O’Gorman, J. P. 2019. Elasmosaurid phylogeny and paleobiogeography, with a reappraisal of *Aphrosaurus furlongi* from the Maastrichtian of the Moreno Formation. Journal of Vertebrate Paleontology 39(5, e1692025):24 pp.

O’Keefe, F. R. 2008. Cranial anatomy and taxonomy of *Dolichorhynchops bonneri* new combination, a polycotylid (Sauropterygia: Plesiosauria) from the Pierre Shale of Wyoming and South Dakota. Journal of Vertebrate Paleontology 28(3):664–676.

O’Keefe, F. R., R. A. Otero, S. Soto-Acuña, J. P. O’Gorman, S. J. Godfrey, and S. Chatterjee. 2017. Cranial anatomy of *Morturneria seymourensis* from Antarctica, and the evolution of filter feeding in plesiosaurs of the Austral Late Cretaceous. Journal of Vertebrate Paleontology 37(4:e1347570):13 pp.

Oksanen, J., F. G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, E. Szoecs, and H. Wagner. 2019. vegan: Community ecology package. R package version 2.5-7. Available at https://CRAN.R-project.org/package=vegan.

Olsson, O., T. Fransson, and K. Larsson. 1999. Post-fledgling migration of common murres *Uria aalge* in the Baltic Sea: Management implications. Ecography 22(3):233-239.

Otero, R. A. 2016. Taxonomic reassessment of *Hydralmosaurus* as *Styxosaurus*: new insights on the elasmosaurid neck evolution throughout the Cretaceous. PeerJ 4(e1777):60 pp.

Palci, A., M. W. Caldwell, and C. A. Papazzoni. 2013. A new genus and subfamily of mosasaurs from the Upper Cretaceous of northern Italy. Journal of Vertebrate Paleontology 33(3):599-612.

Pearson, R. G. 2010. Species’ distribution modeling for conservation educators and practitioners. Lessons in Conservation 3:54-89.

Peng, J., A. P. Russell, and D. B. Brinkman. 2001. Vertebrate microsite assemblages (exclusive of mammals) from the Foremost and Oldman Formations of the Judith River Group (Campanian) of southeastern Alberta: An illustrated guide. The Provincial Museum of Alberta, Natural History Occasional Paper 25:54 pp.

Peters, S. E., and N. A. Heim. 2010. The geological completeness of paleontological sampling in North America. Paleobiology 36(1):61-79.

Peterson, A. T., J. Soberón, R. G. Pearson, R. P. Anderson, E. Martínez-Meyer, M. Nakamura, and M. B. Araújo. 2012. Ecological Niches and Geographic Distributions; in S. A. Levin and H. S. Horn (eds.), Monographs in Population Biology. Princeton University Press, Princeton, New Jersey, 328 pp.

Phillips, S. J., M. Dudík, and R. E. Schapire. 2004. A maximum entropy approach to species distribution modeling; pp. 655-662 in the Proceedings of the Twenty-first International Conference on Machine Learning, Banff, Canada, 4-8 July 2004.

Phillips, S. J., R. P. Anderson, and R. E. Schapire. 2006. Maximum entropy modeling of species geographic distributions. Ecological Modelling 190(3-4):231-259.

Pimiento, C., B. J. MacFadden, C. F. Clements, S. Varela, C. Jaramillo, J. Velez-Juarbe, and B. R. Silliman. 2016. Geographical distribution patterns of *Carcharocles megalodon* over time reveal clues about extinction mechanisms. Journal of Biogeography 43(8):1645-1655.

Pollock, L. J., R. Tingley, W. K. Morris, N. Golding, R. B. O’Hara, K. M. Parris, P. A. Vesk, and M. A. McCarthy. 2016. Understanding co-occurrence by modelling species simultaneously with a Joint Species Distribution Model (JSDM). Methods in Ecology and Evolution 5(5):397-406.

Prior, G.J., B. Hathway, P. M. Glombick, D. I. Pană, C. J. Banks, D. C. Hay, C. L. Schneider, M. Grobe, R. Elgr, and J. A. Weiss. 2013. Bedrock geology of Alberta, Canada. 1:000000. Alberta Energy Regulator/Alberta Geological Survey Map 600. Alberta Geological Survey Open File Report 2013-02.

Provan, J., G. E. Beatty, S. L. Keating, C. A. Maggs, and G. Savidge. 2009. High dispersal potential has maintained long-term population stability in the North Atlantic copepod *Calanus finmarchicus*. Proceedings of the Royal Society B: Biological Sciences 276(1655):301-307.

R Core Team. 2021. R 4.0.4: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available at https://www.r-project.org/.

Real, R., and J. M. Vargas. 1996. The probabilistic basis of Jaccard's Index of Similarity. Systematic Biology 45(3):380-385.

Rees, J., and J. Lindgren. 2005. Aquatic birds from the Upper Cretaceous (lower Campanian) of Sweden and the biology and distribution of hesperornithiforms. Palaeontology 48(6):1321–1329.

Roberts, L. N. R., and M. A. Kirschbaum. 1995. Paleogeography of the Late Cretaceous of the Western Interior of middle North America – Coal distribution and sediment accumulation. United States Geological Survey Professional Paper 1561:115 pp.

Robinson, L. M. J. Elith, A. J. Hobday, R. G. Pearson, B. E. Kendall, H. P. Possingham and A. J. Richardson. 2011. Pushing the limits in marine species distribution modelling: lessons from the land present challenges and opportunities. Global Ecology and Biogeography 20(6):789-802.

Rovelli, R., and C. Myers. 2016. Using PaleoENM to determine the effects of available ecological niche size on extinction susceptibility across the K/Pg extinction in the Mississippi Embayement [sic]. Geological Society of America Abstracts with Programs 48(7):287-2.

Rovelli, R., and C. Myers. 2018. The distal effects of available suitable habitat on extinction potential in cephalopods and other mollusks across the K/Pg in the Atlantic Coastal Plain. Geological Society of America Abstracts with Programs 50(6):163-11.

Royle, J. A., and W. A. Link. 2006. Generalized site occupancy models allowing for false positive and false negative errors. Ecology 87(4):835-841.

Russell, D. A. 1967. Cretaceous vertebrates from the Anderson River N. W. T. Canadian Journal of Earth Sciences 4(1):21-38.

Sato, T. 2003. *Terminonatator ponteixensis*, a new elasmosaur (Reptilia; Sauropterygia) from the Upper Cretaceous of Saskatchewan. Journal of Vertebrate Paleontology 23(1):89-103.

Sato, T., and K. Tanabe. 1998. Cretaceous plesiosaurs ate ammonites. Nature 394:629 630.

Sato, T., and X.-C. Wu. 2006. Review of plesiosaurians (Reptilia: Sauropterygia) from the Upper Cretaceous Horseshoe Canyon Formation in Alberta, Canada. Paludicola 5(4):150-169.

Sato, T., D. A. Eberth, E. L. Nicholls, and M. Manabe. 2005. Plesiosaurian remains from non-marine to paralic sediments; pp. 249-276 in P. J. Currie and E. B. Koppelhus (eds.), Dinosaur Provincial Park: A Spectacular Ancient Ecosystem Revealed, Chapter 14. Indiana University Press, Bloomington, Indiana.

Schumacher, B. A., and J. E. Martin. 2016. *Polycotylus latipinnis* Cope (Plesiosauria, Polycotylidae), a nearly complete skeleton from the Niobrara Formation (Early

Campanian) of Southwestern South Dakota. Journal of Vertebrate Paleontology 36(1):15 pp.

Schumacker, R., and S. Tomek. 2013. Understanding Statistics Using R. Springer, New York, 289 pp.

Schwimmer, D. R., J. D. Stewart, and G. D. Williams. 1994. Giant fossil coelacanths of the Late Cretaceous in the eastern United States. Geology 22:503-506.

Schwimmer, D. R., J. D. Stewart, and G. D. Williams. 1997. Scavenging by sharks of the genus *Squalicorax* in the Late Cretaceous of North America. PALAIOS 12(1):71-83.

Scotese, C.R. 2016. PALEOMAP PaleoAtlas for GPlates and the PaleoData Plotter Program, PALEOMAP Project, Available at https://www.earthbyte.org/paleomap-paleoatlas-for-gplates/. Accessed October 29, 2018.

Scott, B., and P. Anderson. 2021. Identifying competitive exclusion in the vertebrate fossil record: lessons from early vertebrate morphometrics; pp. 33-34 in A. M. Murray, H. Street, and R. B. Holmes (eds.), Proceedings of the 9th Annual Meeting of the Canadian Society of Vertebrate Paleontology, Online, 26-28 May 2021. Vertebrate Anatomy Morphology Palaeontology 9.

Shaw, D. J., Nicolas, M. P. B., and Chow, N. 2017: Stratigraphy and geochemistry of the Cretaceous Boyne Member, Carlile Formation, in the Manitoba Potash Corporation core at 3-29-20-29W1, southwestern Manitoba (parts of NTS 65K1); pp. 173–182 in Report of Activities 2017. Manitoba Growth, Enterprise and

Trade, and the Manitoba Geological Survey, Winnipeg, Manitoba, Canada. Report GS2017-15.

Shealer, D. A. 2002. Foraging behavior and food of seabirds; pp. 137-177 in E. A. Schreiber and J. Burger (eds.), Biology of Marine Birds. CRC Press, Boca Raton, Florida, 722 pp.

Shimada, K., and D. J. Cicimurri. 2005. Skeletal anatomy of the Late Cretaceous shark, *Squalicorax* (Neoselachii: Anacoracidae). Paläontologische Zeitschrift 79:241-261.

Shimada, K., and D. J. Cicimurri. 2006. The oldest record of the Late Cretaceous anacoracid shark, *Squalicorax pristodontus* (Agassiz), from the Western Interior, with comments on *Squalicorax* phylogeny; pp. 177-184 of S. G. Lucas and R. M. Sullivan (eds.), Late Cretaceous Vertebrates from the Western Interior. Authority of the State of New Mexico, Albuquerque, New Mexico. New Mexico Museum of Natural History and Science Bulletin 35.

Shimada, K., and H. D. Hanks. 2020. Shark-bitten hesperornithiform bird bone from a Turonian (Upper Cretaceous) marine deposit of northeastern South Dakota, U.S.A. Transactions of the Kansas Academy of Science, 123(3-4):414-418.

Shimada, K. S., R. E. Chandler, O. L. T. Lam, T. Tanaka, and David J. Ward. 2017. A new elusive otodontid shark (Lamniformes: Otodontidae) from the lower Miocene, and comments on the taxonomy of otodontid genera, including the 'megatoothed' clade. Historical Biology 29(5):704-714.

Shufeldt, R. W. 1915. The fossil remains of a species of *Hesperornis* found in Montana. The Auk 32(3):290-294.

Shurr, G. W., and J. Reiskind. 1984. Stratigraphic framework of the Niobrara Formation (Upper Cretaceous) in North and South Dakota: pp. 205-219 in D. F. Stott and D. J. Glass (eds.), The Mesozoic of Middle North America. Canadian Society of Petroleum Geologists Memoir 9.

Simpfendorfer, C. A., A. B. Goodreid, and R. B. McAuley. 2001. Size, sex and geographic variation in the diet of the tiger shark, *Galeocerdo cuvier*, from Western Australian waters. Environmental Biology of Fishes 61:37-46.

Slattery, J. S., P. J. Harries, and A. L. Sandness. 2018. Do marine faunas track lithofacies? Faunal dynamics in the Upper Cretaceous Pierre Shale, Western Interior, USA. Palaeogeography, Palaeoclimatology, Palaeoecology 496:205-224.

Slattery, J. S., W. A. Cobban, K. C. McKinney, P. J. Harries, and A. L. Sandness. 2015. Early Cretaceous to Paleocene paleogeography of the Western Interior Seaway: The interaction of eustasy and tectonism; pp. 22-60 in M. Bingle-Davis (ed.), Wyoming Geological Association Guidebook, 68th Annual Field Conference, Cretaceous Conference: Evolution and Revolution, Casper, Wyoming.

Slingerland, R., L. R. Kump, M. A. Arthur, P. J. Fawcett, B. B. Sageman, and E. J. Barron. 1996. Estuarine circulation in the Turonian Western Interior seaway of North America. Geological Society of America Bulletin 108(7):941-952.

Smith, G. J., and L. R. G. DeSantis. 2020. Extinction of North American *Cuvieronius* (Mammalia: Proboscidea: Gomphotheriidae) driven by dietary resource competition with sympatric mammoths and mastodons. Paleobiology 46(1):41–57.

Stigall Rode, A. L., and B. S. Lieberman. 2005. Using environmental niche modeling to study the Late Devonian biodiversity crisis; pp. 93-179 in D. J. Over, J. R. Morrow, and P. B. Wignall (eds.), Understanding Late Devonian and Permian-Triassic Biotic and Climatic Events: Towards an Integrated Approach. Elsevier B. V., Amsterdam, The Netherlands. Developments in Palaeontology and Stratigraphy 20.

Stockwell, D., and D. Peters. 1999. The GARP modelling system: problems and solutions to automated spatial prediction. International Journal of Geographical Information Science 13(2):143-158.

Stott, D. F., W. G. E. Caldwell, D. J. Cant, J. E. Christopher, J. Dixon, E. H. Koster, D. H. McNeil, and F. Simpson. 1993. Subchapter 4I: Cretaceous; pp. 358-438 in D. F. Stott, and J. D. Aitken (eds.), Sedimentary Cover of the Craton in Canada. Geological Survey of Canada and Geological Society of America, Canada Communications Group – Publishing, Ottawa, Canada. The Geology of North America D-1.

Street, H. P. 2020. Abundant juvenile plesiosaur fossils from an upper Campanian marine reptile bonebed in Saskatchewan, Canada; pp. 56-57 in A. M. Murray, V. Arbour, and R. B. Holmes (eds.), Proceedings of the 8th Annual Meeting of the Canadian Society of Vertebrate Paleontology, Victoria, B. C., 6-8 June 2020. Vertebrate Anatomy Morphology Palaeontology 8.

Svenning, J.-C., C. Fløjgaard, K. A. Marske, D. Nógues-Bravo, and S. Normand. 2011. Applications of species distribution modeling to paleobiology. Quaternary Science Reviews 30(21-22):2930-2947.

Tanaka, T., Y. Kobayashi, K., K. Kurihara, A. R. Fiorillo, and M. Kano. 2018. The oldest Asian hesperornithiform from the Upper Cretaceous of Japan, and the phylogenetic reassessment of Hesperornithiformes. Journal of Systematic Palaeontology 116(8):689-709.

Tavares, D. C., J. F. Moura, A. Merico, and S. Siciliano. 2020. Mortality of seabirds migrating across the tropical Atlantic in relation to oceanographic processes. Animal Conservation 23(3):307-319.

Thiebault, A., M. Semeria, C. Lett, and Y. Tremblay. 2016. How to capture fish in a school? Effect of successive predator attacks on seabird feeding success. Journal of Animal Ecology 85(1):157-167.

Timm, K. K., and S. A. Sonnenberg. 2018. Geochemical and micropaleontological evidence of paleoenvironmental change in the Late Cretaceous Western Interior Seaway from the Niobrara to the Pierre Shale Formation. The Mountain Geologist 55(4):145-176.

Tyler, C. L., and L. R. Leighton. 2011. Detecting competition in the fossil record: Support for character displacement among Ordovician brachiopods. Palaeogeography, Palaeoclimatology, Palaeoecology 307(1-4):205–217.

Tyre, A. J., B. Tenhumberg, S. A. Field, D. Niejalke, K. Parris, and H. P. Possingham. 2003. Improving precision and reducing bias in biological surveys: Estimating false-negative error rates. Ecological Applications 13(6):1790-1801.

Uhen, M. D., and N. D. Pyenson. 2007. Diversity estimates, biases, and historiographic effects: Resolving cetacean diversity in the Tertiary. Palaeontologia Electronica 10(2):22 pp.

Varela, S., J. M. Lobo, and J. Hortal. 2011. Using species distribution models in paleobiogeography: A matter of data, predictors and concepts. Palaeogeography, Palaeoclimatology, Palaeoecology 310(3-4):451-463.

Vaughn, R. L., B. Würsig, D. S. Shelton, L. L. Timm, and L. A. Watson. 2008. Dusky dolphins influence prey accessibility for seabirds in Admiralty Bay, New Zealand. Journal of Mammalogy 89(4):1051-1058.

Veit, R. R., and N. M. Harrison. 2017. Positive interactions among foraging seabirds, marine mammals and fishes and implications for their conservation. Frontiers in Ecology and Evolution 5(121):8 pp.

Vilhena, D. A., and A. B. Smith. 2013. Spatial bias in the marine fossil record. PLoS ONE 8(10, e74470):7 pp.

Vlietstra, L. S. 2005. Spatial associations between seabirds and prey: effects of large-scale prey abundance on small-scale seabird distribution. Marine Ecology Progress Series 291:275-287.

Wall, P. D., L. C. Ivany, and B. H. Wilkinson. 2009. Revisiting Raup: exploring the influence of outcrop area on diversity in light of modern sample-standardization techniques. Paleobiology 35(1):146-167.

Walls, B. J., and A. L. Stigall. 2011. Analyzing niche stability and biogeography of Late Ordovician brachiopod species using ecological niche modeling. Palaeogeography, Palaeoclimatology, Palaeoecology 299:15–29.

Warren, R., R. E. Smith, and A. K. Cybenko. 2011. Use of Mahalanobis distance for detecting outliers and outlier clusters in markedly non-normal data: A vehicular traffic example. Air Force Research Laboratory, Wright-Patterson Air Force Base, OH. DTIC Interim Report AFRL-RH-WP-TR-2011-0070:60 pp.

Waterson, A. M., D. N. Schmidt, P.J. Valdes, P. A. Holroyd, D. B. Nicholson, A. Farnsworth, and P. M. Barrett. 2016. Modelling the climatic niche of turtles: a deep-time perspective. Proceedings of the Royal Society B: Biological Sciences 283(1839):8 pp.

Welles, S. and Bump, J. 1949. *Alzadasaurus pembertoni*, a new elasmosaur from the Upper Cretaceous of South Dakota. Journal of Paleontology 23(5):521-535.

Wells, B. K., J. A. Santora, M. J. Henderson, P. Warzybok, J. Jahncke, R. W. Bradley, David D. Huff, I. D. Schroeder, P. Nelson, J. C. Field, and D. G. Ainley. 2017. Environmental conditions and prey-switching by a seabird predator impact juvenile salmon survival. Journal of Marine Systems 174:54-63.

Whittingham, M. J., P. A. Stephens, R. B. Bradbury, and R. P. Freckleton. 2006. Why do we still use stepwise modelling in ecology and behaviour? Journal of Animal Ecology 75(5):1182–1189.

Wilson, L. E. 2019. A bird’s eye view: Hesperornithiforms as environmental indicators in the Late Cretaceous Western Interior Seaway. 122(3-4):193-213.

Wilson, L. E., and K. Chin. 2014. Comparative osteohistology of *Hesperornis* with reference to pygoscelid penguins: the effects of climate and behaviour on avian bone microstructure. Royal Society Open Science 1(3), 140245:16 pp.

Wilson, L. E., K. Chin, and S. Cumbaa. 2016. A new hesperornithiform (Aves) specimen from the Late Cretaceous Canadian High Arctic with comments on high-latitude hesperornithiform diet. Canadian Journal of Earth Sciences 53:1476-1483.

Wilson, L. E., K. Chin, S. Cumbaa, and G. Dyke. 2011. A high latitude hesperornithiform (Aves) from Devon Island: palaeobiogeography and size distribution of North American hesperornithiforms. Journal of Systematic Palaeontology 9(1):1-15.

Young, M. A., P. J. Iampietro, R. G. Kvitek, and C. D. Garza. 2011. Multivariate bathymetry derived generalized linear model accurately predicts rockfish distribution on Cordell Bank, California, USA. Marine Ecology Progress Series 415:247-261.

Zipkin, E. F., J. Andrew Royle, Deanna K. Dawson, and Scott Bates. 2010. Multi-species occurrence models to evaluate the effects of conservation and management actions. Biological Conservation 143(2):479-484.

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