

# Out of the dark: 350 million years of conservatism and evolution in diel activity patterns in vertebrates

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Many animals are active only during a particular time (e.g., day vs. night), a partitioning that may have important consequences for species coexistence. An open question is the extent to which this diel activity niche is evolutionarily conserved or labile. Here, we analyze diel activity data across a phylogeny of 1914 tetrapod species. We find strong phylogenetic signal, showing that closely related species tend to share similar activity patterns. Ancestral reconstructions show that nocturnality was the most likely ancestral diel activity pattern for tetrapods and many major clades within it (e.g., amphibians, mammals). Remarkably, nocturnal activity appears to have been maintained continuously in some lineages for ~350 million years. Thus, we show that traits involved in local-scale resource partitioning can be conserved over strikingly deep evolutionary time scales. We also demonstrate a potentially important (but often overlooked) metric of niche conservatism. Finally, we show that diurnal lineages appear to have faster speciation and diversification rates than nocturnal lineages, which may explain why there are presently more diurnal tetrapod species even though diurnality appears to have evolved more recently. Overall, our results may have implications for studies of community ecology, species richness, and the evolution of diet and communication systems.

**KEY WORDS:** Diel activity, diversification, niche conservatism, phylogeny, species richness.

The niche is a central concept in ecology, evolution, and biogeography. The niche describes both the abiotic conditions where a species can occur (the Grinnellian niche), and the resources that it requires from some species and provides to other species (the Eltonian niche; Hutchinson 1957; Soberón 2007; Holt 2009). A potentially important but sometimes neglected aspect of the niche is the diel activity niche (reviewed by Kronfeld-Schor and Dayan 2003; Hut et al. 2012). For many groups, distinct sets of species may be active during the day versus night. For example, it is well known that most bats and moths are active at night, whereas most birds and butterflies are active by day. Each set of species may be adapted to very different abiotic conditions (e.g., light, temperature; Levy et al. 2012), and may use distinct sets of resources (e.g., Kronfeld-Schor and Dayan 1999). Thus, the diel activity niche spans both the Grinnellian and Eltonian aspects of the niche.

In recent years, there has been increasing interest in the evolution and conservatism of ecological niches, and the implications

of both for diverse topics in ecology, evolutionary biology, biogeography, and conservation biology (e.g., Wiens et al. 2010; Peterson 2011; Crisp and Cook 2012). Patterns of evolution and conservatism in the diel niche may be particularly important for the structure and assembly of communities, given that different sets of species may be active by day and night in a given location (Kronfeld-Schor and Dayan 2003). However, much attention on niche evolution and niche conservatism has focused on large-scale climatic niches (e.g., Peterson 2011), rather than on traits that allow species to partition resources and coexist at the local scale (but with some exceptions; e.g., Cavender-Bares et al. 2009; Olalla-Tárraga et al. 2017). Addressing the evolution of the diel niche may provide further insights into whether factors that impact local-scale species interactions are conserved or labile, and over what timescales.

Diel niches can be highly conserved in some cases and highly labile in others. For example, Roll et al. (2006) found that diel activity was strongly conserved in rodents, using data

from 700 species and a goodness-of-fit test that compared the diel activities in each clade of rodents to those of the entire order. In contrast, considerable flexibility in diel activity has been documented within species in response to variables like predation (e.g., Kronfeld-Schor and Dayan 2008; Monterroso et al. 2013), seasonal climate shifts (e.g., Wilson et al. 2009; Abom et al. 2012), and human impacts (e.g., Kitchen et al. 2000; Rasmussen and MacDonald 2012). Nevertheless, based on their review of studies of individual species, Kronfeld-Schor and Dayan (2003) concluded that major shifts in diel activity due to competition or predation were rare. Thus, they suggested that shifts between nocturnal and diurnal activity within species were uncommon, even though there were many shifts in temporal activity documented within each category (e.g., different parts of the night in nocturnal species). They suggested that the rarity of these major shifts might be due to long-term evolutionary constraints. These constraints, if present, might be related to thermal tolerances, visual systems, or other factors (see Discussion). However, to our knowledge, no studies have tested this general idea (i.e., long-term conservatism or constraint in diel activity niches) by analyzing the evolution of diel niches among species at relatively deep time scales.

In this study, we analyze the evolution of the diel niche across major clades of terrestrial vertebrates (tetrapods; i.e., amphibians, birds, mammals, reptiles). Interestingly, despite many large-scale studies within these clades (e.g., amphibians, mammals; Buckley et al. 2010; Olalla-Tárraga et al. 2011, 2017), relatively few studies of niche evolution and conservatism have spanned these major tetrapod clades (if any). Here, we assemble a time-calibrated phylogeny and accompanying diel activity data from the literature for 1914 tetrapod species. We test for phylogenetic conservatism in the diel niche (i.e., closely related species sharing similar traits), using Pagel's (1999) lambda. We then analyze the major patterns of change in the diel niche across tetrapods. We also include a simple but potentially important metric of niche conservatism that has been largely overlooked in the recent literature: the maximum amount of time that an ecological trait has been maintained in a clade.

Ours may be the first study to address large-scale patterns of evolution and conservatism in diel niches across tetrapods (or any major group). Nevertheless, some previous studies have analyzed patterns of diel activity within some tetrapod clades (e.g., rodents; Roll et al. 2006; gekkotan lizards; Gamble et al. 2015). Another set of studies have inferred ancestral diel activity for particular tetrapod clades using less direct evidence of diel activity, such as eye morphology (e.g., indicating ancient nocturnality in mammals, synapsids, and dinosaurs; Schmitz and Montani 2011; Hall et al. 2012; Angielczyk and Schmitz 2014), and visual pigments (e.g., absence of RH2 and SW2 in mammals and RH2 in amphibians, possibly indicating ancestral nocturnality in these groups; Bowmaker 2008; Gerkema et al.

2013). Similarly, Chang et al. (2002) inferred that archosaurs (i.e., birds plus crocodylians) were ancestrally nocturnal based on ancestral sequences and functional analyses of the rhodopsin gene. Overall, this latter set of studies suggests that many deep nodes within tetrapods may have been ancestrally nocturnal. However, these studies inferred diel activity only indirectly, for only one or two nodes, sampled relatively few species, and did not use model-based reconstruction methods (e.g., maximum likelihood). Here, we address conservatism and evolution in diel niches across all major groups of tetrapods using data on diel activity from >1900 species and using model-based methods for testing phylogenetic signal and reconstructing ancestral nodes.

Our results show that the diel activity niche is strongly conserved among vertebrate clades. We also find that primarily nocturnal activity seems to be ancestral for tetrapods, and has been maintained in some lineages for at least 350 million years. Our results also suggest that strictly diurnal species proliferate more rapidly than nocturnal species. This finding may explain why diurnal species currently outnumber nocturnal species, even though strict diurnality appears to have evolved more recently in tetrapods.

## Methods

### TREE CONSTRUCTION

Time-calibrated trees for major tetrapod clades were obtained from several primary literature sources and then combined (e.g., Jaffe et al. 2011; Oaks 2011; Jetz et al. 2012; Pyron and Wiens 2013; Pyron and Burbrink 2014; Rolland et al. 2014). In general, we used the most recent and comprehensive time-calibrated phylogeny available for each group at the time that we compiled the tree. The study of vertebrate phylogeny by Alfaro et al. (2009) was used as the backbone of the combined tree. This topology and associated broad-scale divergence dates are also supported by recent phylogenomic analyses (but including fewer taxa), including both concatenated and species-tree analyses (Chiari et al. 2012). Nontetrapod taxa were pruned from this backbone tree and more detailed time-calibrated phylogenies within each tetrapod clade were added manually. These included trees for amphibians (Pyron and Wiens 2013), crocodylians (Oaks 2011), turtles (Jaffe et al. 2011), and squamates (Pyron and Burbrink 2014). For mammals, we used a tree from Rolland et al. (2014) that redates the extensive, species-level tree of Bininda-Emonds et al. (2007) utilizing selected nodes from the higher-level time-calibrated phylogeny from Meredith et al. (2011). For birds, we used two trees from Jetz et al. (2012), but only including those species that were incorporated into their tree based on sequence data, and not taxonomy alone. One tree used the backbone, higher level tree from Ericson et al. (2006) and the other that from Hackett et al. (2008). Specifically, we generated a list of species and then obtained

a set of 100 trees for each backbone tree from the website (<http://birdtree.org>) associated with Jetz et al. (2012). We then built a majority-rule consensus tree from each set of 100 trees, using TreeAnnotator and FigTree (associated with the software package BEAST; Drummond and Rambaut 2007). These trees had relatively few weakly resolved branches, given that we only selected bird species for which sequence data were available (in Jetz et al. 2012). Overall, this resulted in two versions of the combined tetrapod tree and all analyses were conducted on both trees. For brevity, we refer to these as the Ericson and Hackett trees, but note that topologies differ only within birds (although use of different topologies in birds sometimes led to differences in rates that caused different reconstructions for some nodes outside of birds). Only species with diel activity data were included in these trees.

To combine the trees across major clades, we simply pasted each of these six subtrees into the newick version of the higher level tree of Alfaro et al. (2009), replacing the segment of the tree for the sampled species from that clade. We then adjusted the length of the stem-group branch from each of these major lineages, such that the crown-group ages corresponded to those in these well-sampled subtrees rather than those from Alfaro et al. (2009). These minor adjustments led to minute differences in branch lengths that prevented trees from being strictly ultrametric. To strictly ultrametricize the trees, we used the polytomy resolver of Kuhn et al. (2011). This generates a file that is implemented in BEAST 1.5.4 (Rambaut and Drummond 2007). BEAST was then run without data for 2000 generations, with the constraint that the original topology is maintained and any differences in branch lengths must be small ( $<10,000$  years). This corrected for rounding errors in branch lengths. The final phylogenies are available as Supplementary Files S1–S4. Supporting Information files will be made available on Dryad.

We acknowledge that we did not account for phylogenetic uncertainty within most groups (except birds). However, many of the large-scale relationships within these groups are relatively well-resolved. Furthermore, our results on phylogenetic signal suggest that closely related species share similar diel niche trait values (such that differences in topology among closely related species should have little impact on our results). Also, a large set of time-calibrated trees was simply unavailable for many groups.

Finally, we are aware that newer phylogenies are being generated within some groups (although these are often less comprehensive than those used here). However, many new phylogenies are generally similar to those used here (e.g., squamates; Zheng and Wiens 2016), and so should not overturn our conclusions. Higher-level bird phylogeny has been contentious in recent studies (e.g., Jarvis et al. 2014; Prum et al. 2015), but we do explore alternative trees in this group, and these recent phylogenomic trees did not contain sufficient species sampling to allow their use

here. Furthermore, most variation in diel activity patterns in birds is not among these higher level clades (e.g., Figs. S1–S8).

## DATA COLLECTION

Data on diel activity patterns were compiled largely from books, original papers, and some secondary papers (e.g., Meiri et al. 2012). Each species was initially assigned one of four character states: diurnal, nocturnal, crepuscular, or arrhythmic. The states were delimited following standard definitions (e.g., Schmitz and Montani 2011). Specifically, diurnal species were those described in the literature as being solely or primarily active after sunrise and before sunset. Nocturnal species were those characterized as solely or primarily active after sunset and before sunrise. Crepuscular species were those described as primarily active during twilight or in the early morning and at dusk. However, species that were active both during twilight as well as at night were scored as nocturnal. Similarly, those active both at twilight and during the day were considered diurnal. We used these criteria because many species that are primarily nocturnal or diurnal may also be active during the beginning or end of the day or night. Given these criteria, relatively few species were considered crepuscular (26 of 1914 species). Finally, species were considered to be arrhythmic (i.e., cathemeral) if they were described as similarly active during the day and night, or if they changed their primary diel activity between day and night seasonally. However, relatively few of the sampled species were arrhythmic (120 of 1914).

For some species, an explicit description of the diel niche was not found but data were nevertheless provided on foraging, calling, roosting, and/or sleeping times. In these cases, categorizing species was relatively straightforward. In species that routinely burrow, the time of day with the most above-ground activity was used to assess diel activity. Species were excluded if adequate activity-pattern data could not be found. We found few (if any) conflicts in the literature about the diel activity pattern of any given species, perhaps because most species were primarily nocturnal or diurnal by our criteria.

Within each major clade of tetrapods (i.e., amphibians, birds, crocodylians, lepidosaurs, mammals, turtles), we generally sampled species to represent the higher taxa within each clade (e.g., orders, families) in approximate proportion to their relative species richness within the major clade. Within each of these higher taxa, species were then selected based on their inclusion in available phylogenies and on the availability of diel activity data.

We obtained diel activity data for 1914 tetrapod species, all of which were included in the phylogeny (Table 1). These included 514 amphibians, 508 lepidosaurs, 88 turtles, 549 birds, 19 crocodylians, and 236 mammals. Data for each species and supporting references are in File S5.

We recognize that not everyone may agree with the characterization of every species, but we have based our coding of species

**Table 1.** Percentage of sampled species with different diel activity states in each major tetrapod clade, along with the total number of sampled species, and the number of described extant species in each clade.

Clade	Percentage of nocturnal	Percentage of diurnal	Percentage of crepuscular	Percentage of arrhythmic	Sampled species	Extant species
Amphibians	79.77	11.67	0.58	7.98	514	7294
Mammals	67.80	17.80	2.97	11.44	236	5487
Lepidosaurs	33.66	58.07	1.57	6.69	508	9557
Turtles	14.78	75.00	2.27	7.95	88	327
Crocodylians	100.00	0.00	0.00	0.00	19	25
Aves	6.92	89.98	1.09	2.01	549	9993

on explicit literature sources, rather than anecdotal observations or conventional wisdom about particular species. Furthermore, if there are errors in coding some individual species (e.g., due to mischaracterization of activity patterns in previous papers), they should have little impact on the broad-scale patterns we emphasize here.

Species sampling within clades was largely proportional to their richness (Table 1). Turtles and crocodylians were somewhat oversampled relative to other clades, but this should be of limited consequence given their low richness overall. Therefore, the main analyses included all 1914 species. We conducted preliminary analyses in which the proportional sampling of turtles and crocodylians was reduced to a level similar to the other groups (~5% of overall richness). We included one crocodylian and 16 turtle species for a total of 1824 species. Turtle species were selected to represent all 14 families, with one added species each for the two most species-rich families (Geoemydidae, Testudinidae). To select species independently of diel activity, turtle species were selected to represent the type genus of each family whenever possible (i.e., independent of diel activity) and also to represent major clades within Geoemydidae and Testudinidae. All sampled crocodylians share the same diel activity state. However, these preliminary analyses gave similar results to those using all species, and we only present results with all 1914 species.

Amphibians might also be considered slightly overrepresented relative to other clades. However, the number of described amphibians is still increasing rapidly, with ~2000 species added in the past ~12 years (2004–2016; AmphibiaWeb 2016). Therefore, we assumed the actual number of amphibians is at least as high as the number of described bird or lepidosaur species.

In theory, it would be possible to include more species within these clades. On the other hand, the number included here is computationally tractable for the approaches used here. Moreover, our results show strong phylogenetic signal in diel activity (see below). Thus, additional species should tend to share the same state as their closest relatives in our tree, and should therefore not overturn our conclusions. Some analyses (e.g., BiSSE, see below) might be problematic with too few species, because of limited

statistical power to distinguish between models (FitzJohn et al. 2009). However, we often found large differences (>15 Akaike information criterion [AIC]) between the best-fitting model for a given analysis and the second best model (see next). Thus, limited taxon sampling clearly did not prevent us from detecting strong differences in rates between models.

#### TESTING FOR PHYLOGENETIC SIGNAL

To test for phylogenetic signal in diel activity patterns, we first estimated values of Pagel's (1999) lambda using the `fitDiscrete` function in the R package *geiger* version 2.0.6 (Harmon et al. 2008; Pennell et al. 2014). Note that all R scripts are provided in Supplementary Files S6–S9, and all datasets analyzed are in Supplementary Files S10–S13. Lambda measures the fit of the data to a Brownian motion model in which trait evolution closely matches the phylogeny, with higher values of lambda (closer to 1) indicating higher phylogenetic signal, and lower values (closer to zero), indicating low signal (Pagel 1999). We compared the fit of the data to a model based on the estimated lambda value (EL model) to that for a white noise model (WN), in which there is no phylogenetic signal. The presence of phylogenetic signal indicates that closely related species share similar trait values, a key component of niche conservatism (review in Wiens et al. 2010). In contrast, stronger support for the WN model would reject the presence of phylogenetic signal and niche conservatism. A third possibility is that there is low phylogenetic signal but no support for the WN model because of strong conservatism across the tree (Ornstein-Uhlenbeck model, or OU). However, we do not know of a way to implement the OU model with discrete traits. Most importantly, our results (see below) show strong phylogenetic signal, strongly suggesting that the OU model would not be supported. Likelihoods were compared using the AIC. Following Burnham and Anderson (2002), AIC differences >4 between the best-fitting model and the model with the next best fit were considered strong support for the best-fitting model.

We recognize that some authors have questioned whether phylogenetic signal is relevant to niche conservatism (e.g., Losos 2008). However, this argument is based largely on the idea that

signal and rate are uncoupled. Yet, phylogenetic signal will reflect evolutionary rate for discrete characters (e.g., Revell et al. 2008; p. 598), such as diel activity. Furthermore, a review of this debate by many authors concluded that phylogenetic signal can indicate niche conservatism, because strong signal indicates that closely related species will share similar trait values (Wiens et al. 2010). However, those authors recognized that there could be niche conservatism (e.g., strong stasis) without signal, as under an OU model. Again, our results here support very strong signal, making this latter possibility very unlikely.

As an alternative test for phylogenetic signal in diel activity patterns, we estimated the  $D$ -statistic (Fritz and Purvis 2010), which was explicitly designed for testing for phylogenetic signal in discrete (binary) traits.  $D$ -statistics were estimated using the `phylo.d` function in the R package *caper* version 0.5.2 (Orme 2013). The  $D$ -value is the sum of state changes along branches for a binary trait, with smaller values indicating fewer state changes and supporting the hypothesis that a trait is phylogenetically conserved. The `phylo.d` function compares the estimated  $D$ -value to alternative  $D$  values generated with simulated data based on models of Brownian motion (strong phylogenetic signal) and WN (no phylogenetic signal). The estimated  $D$ -value is then scaled according to the simulated values, such that a  $D$ -statistic of 0 indicates the trait conservatism expected under Brownian motion and a value of 1 indicates a random distribution.  $P$  values are calculated to determine if the  $D$ -statistic is significantly different from simulated  $D$  values under the Brownian motion and WN models.

### ANCESTRAL STATE RECONSTRUCTION

The evolution of diel activity states across the tree was analyzed using ancestral state reconstructions with maximum likelihood. However, these analyses were conducted after recoding diel activity as a binary character (nocturnal vs. diurnal). This was done for two reasons. First, simulations have shown that likelihood analyses (i.e., BiSSE) can yield misleading results if states are present in <10% of the species (Davis et al. 2013). Indeed, initial analyses treating diel activity as a four-state character led to reconstructions with nonsensical results, with the two rare states (arrhythmic, crepuscular) reconstructed in ancestors of clades that were dominated by the alternate, more common states. Second, present implementations of likelihood methods that allow for rate heterogeneity across trees (HiSSE, corHMM; see next) can only be used if characters have only two states.

We treated diel activity as a two-state character by coding all crepuscular and arrhythmic species as either nocturnal or diurnal. We generated a “maximum diurnal” coding scheme in which all crepuscular and arrhythmic species were categorized as diurnal and a “maximum nocturnal” coding, which grouped crepuscular and arrhythmic species in the nocturnal category.

Ancestral state reconstructions can potentially be influenced by the effect of a given character state on speciation and extinction (Maddison et al. 2007). To account for this, we initially used the BiSSE approach in preliminary analyses, as implemented in the R package *diversitree* version 0.9-7 (FitzJohn 2012). However, we preferred to use HiSSE, the hidden state speciation and extinction model (version 1.8, Beaulieu and O’Meara 2016) for two reasons. First, some concerns have been noted about spurious correlations between traits and diversification rates generated in BiSSE (Maddison and FitzJohn 2015; Rabosky and Goldberg 2015). Unlike BiSSE, HiSSE allows a binary character to evolve independently of the diversification process and allows diversification rates to vary across the phylogeny. Specifically, HiSSE allows inclusion of a correlated and unobserved (i.e., hidden) character in the model that can influence diversification rates and reconstructions (but which is independent of the observed character). Including variation in rates is important given many distantly related clades included on the same tree, because homogeneity in these parameters is unlikely (King and Lee 2015). Second, and most importantly, use of HiSSE allowed us to compare the fit of a BiSSE-like model (state-dependent speciation and extinction, with no hidden state) to one with a hidden state. The model with the hidden state was supported (see Results). Therefore, our results reject use of a standard BiSSE model.

Using the AICc (Burnham and Anderson 2002), we compared the fit of five different models. We ran two BiSSE-type models: a restricted BiSSE model with constrained speciation and extinction rates and two transition rates (implemented in HiSSE, referred to as the HiSSE two-state model) and a full BiSSE model (two observed states, no rates constrained). We also compared two null HiSSE models in which observed states (0, 1: diurnal, nocturnal) were paired with hidden states (A, B) but rates were varied across hidden states only, effectively ignoring the observed states (i.e.,  $1A = 0A$ ,  $1B = 0B$ ). One of the null models incorporated two hidden states (Null2 model) with the two observed states and the other incorporated four hidden states (Null4 model). By using four hidden states, the Null4 model uses the same number of states as the full HiSSE model (i.e., 0A, 1A, 0B, 1B), but without incorporating the observed trait data. We also ran a full HiSSE model that pairs the two observed states with two hidden states and allows separate parameters for each of the four possible pairings of observed and hidden states (0A, 1A, 0B, 1B). Comparisons across all five models were done for both trees (Ericson and Hackett trees within birds) and for both the maximum diurnal and maximum nocturnal coding schemes.

The HiSSE analyses were conducted using the default assumption for the root state (“madfitz,” see FitzJohn et al. 2009). Once the best-fitting model was identified, we then tested the fit of this default root prior assumption (madfitz) to one assuming equal likelihood of any state at the root (equal), based on



comparisons of the AIC for the same tree and coding method. Finally, we performed our main analyses using the best-fitting root-state assumption. We also estimated ancestral states using nonoptimal root-state assumptions, as alternative analyses.

For all analyses, we explicitly accounted for the incomplete sampling of species (Table 1). To do this, we assumed our tree contained a random sampling of all extant species within each major clade, and that our sampling was independent of diel activity (FitzJohn et al. 2009). All other things being equal, random sampling within each major clade should yield species numbers for each subclade that are proportional to the richness of that subclade within the major clade, and this is how we designed our species-level sampling (and with no a priori selection of species based on their diel activity patterns). The total number of extant tetrapod species was considered to be 32,683, comprising 7294 amphibians (AmphibiaWeb 2014), 327 turtles, 25 crocodylians and 9557 lepidosaurs (Uetz and Hosek 2014), 9993 birds (Jetz et al. 2012), and 5,487 mammals (IUCN 2014). Updates to these numbers should have little impact on *proportional* richness.

As an alternative approach to address heterogeneity in transition rates between states across this large phylogeny, we performed maximum-likelihood ancestral state reconstructions using the corHMM package version 1.20 (Beaulieu et al. 2013). This program allows the observed binary character to be paired with a number of different transition-rate classes treated as hidden states, but it does not account for the effect of states on speciation and extinction rates as in HiSSE. We compared the fit of different numbers of rate classes (from 1 to 5), using AICc values. We used both trees (Ericson and Hackett) and coding schemes (maximum diurnal and nocturnal) under the default root prior assumption of equal weighting for all states at the root (“null”). We then tested the fit of two additional assumptions for the root-state prior (based on the AICc), including “madfitz” (FitzJohn et al. 2009) and “yang” (Yang 2006). This was done on the best-fitting number of rate classes for each tree and coding scheme, which was determined using equal weighting for the root state. Our main analyses were done using the best-fitting root-state assumption, but we also present alternative results using the other two assumptions.

Given the best-fitting model for each approach (HiSSE, corHMM), we then evaluated the reconstructed state at each node for each tree and coding method. To do this, observed states were lumped together such that the marginal likelihoods of the diurnal or nocturnal state include the likelihoods of both hidden-state combinations (e.g., nocturnal = 1A + 1B). A given observable state was considered strongly supported at a given node if it had a proportional likelihood of 0.88 or higher. This corresponds to a difference between the log likelihoods with and without the state present at that node of 2 or more, which is statistically significant using the standard likelihood decision threshold of 2.0.

We recognize that other analyses could have been done, such as Bayesian reconstructions with no hidden states. However, our analyses show that simpler models are rejected for these data. Furthermore, the HiSSE and corHMM analyses have quite different assumptions (e.g., corHMM ignores potential differences in speciation and extinction rates among states), but they still yielded similar ancestral state reconstructions overall.

### TRAIT RETENTION INDEX

Finally, we used ancestral state reconstructions to estimate an alternative index of niche conservatism (called the trait retention index) based on the maximum time that a trait is retained continuously to the present day (Wiens 2015b). Thus, we considered the oldest node with a given state and evaluated whether this state could be traced to the present day through an uninterrupted series of ancestors, all sharing the same state. This index implicitly assumes that there are no unobserved state changes on branches in between reconstructed nodes. Unfortunately, this issue is difficult to address with the methods described thus far (e.g., reconstructions with the HiSSE and corHMM models), because they only estimate states at nodes. To partially address this concern, we also performed stochastic mapping of the evolution of diel activity states (e.g., Huelsenbeck et al. 2003). This approach uses simulations to evaluate whether there might be additional changes on branches, apart from those estimated based on state differences between nodes (but note that this approach shows results of individual simulation replicates, not statistical support for reconstructions on each branch). Stochastic mapping was implemented in *phytools*, version 0.5–38 (Revell 2012). We used the all-rates-different model (ARD) model, with all rates of change between states different, which is most consistent with the best-fitting models from HiSSE. However, note that this simple likelihood model is rejected for these data, and that HiSSE and corHMM models incorporating differences in rates of speciation and extinction between states (and heterogeneity in those rates) have significantly better fit. Therefore, this should be seen primarily as a heuristic exercise. In a similar vein, results from the four-state coding should be taken with considerable caution because of the problem of rare states mentioned above.

We used 25 stochastic simulations for each tree (Ericson, Hackett) and coding strategy (maximum diurnal, maximum nocturnal, four states). Then, for each set of 25 replicates, we evaluated how often the root state (i.e., nocturnality) was retained continuously to the present day in one or more species within each of these clades, and how often that root state was nocturnality. We focused specifically on amphibians and mammals, the two groups which our other reconstructions suggest have retained nocturnality since the tetrapod root (see Results). We also performed likelihood reconstructions with the ARD model to confirm that we obtained broadly similar results to those from HiSSE. We

**Table 2.** Estimated phylogenetic signal in diel activity under different topologies and coding schemes, using the lambda statistic of Pagel (1999).

	Ericson tree	Hackett tree
Four state	0.827	0.782
Maximum diurnal	0.966	0.963
Maximum nocturnal	0.991	0.991

Model-fitting analyses (Table 3) show that the model based on the estimated lambda has the best fit, rejecting a model based on random variation (white noise).

note that it is possible to perform more than 25 replicates, but additional replicates would have been difficult for visualization (given the many taxa per tree). For the stochastic simulations, we estimated the transition-rate matrix. We also estimated the prior on the root state ( $\pi$  = estimated).

## Results

We first estimated the overall number of nocturnal and diurnal species among tetrapods (Table 1). Multiplying our estimated proportions of each activity mode from each clade by the overall richness of that clade (and summing across clades) suggests that there are 13,520 nocturnal species (41.4%), 16,615 diurnal species (50.8%), and that fewer are crepuscular ( $n = 471$ ; 1.4%) and arrhythmic ( $n = 2076$ ; 6.3%). Thus, the majority of tetrapod species are diurnal. Amphibians, mammals, and crocodylians are dominated by nocturnal species, whereas birds, lepidosaurs (i.e., lizards), and turtles are dominated by diurnal species (Table 1). Birds and lepidosaurs are also the most species-rich tetrapod clades (Table 1). Similar proportions were obtained for amniotes only (and excluding crocodylians and turtles) by Schmitz and Montani (2011).

Our results showed strong support for phylogenetic conservatism in diel activity, and rejected the idea that this trait is highly labile and varies randomly among species (Table 2). Across the different trees (Ericson or Hackett; recall that these trees differ only within birds) and coding schemes (4-state, maximum diurnal, maximum nocturnal), diel activity patterns showed strong phylogenetic signal, with Pagel's lambda close to 1 (range: 0.782–0.991), especially using two states (range: 0.96–0.99). The best-fitting model for all trees and coding methods (Table 3) was one based on the EL value. The WN model had dramatically poorer fit, with differences in the AIC consistently  $>1000$ , strongly rejecting the idea that diel activity varies randomly among species across the tree.

Results from the  $D$ -statistic also supported strong conservatism for both trees and binary coding schemes (Table 4). Estimated  $D$  values were not significantly different from zero (the

value expected under a Brownian motion model, with strong phylogenetic signal) but were significantly different from 1 (the value expected under a WN model, with no phylogenetic signal).

Model comparisons strongly supported the full HiSSE model over all simpler models (Table S1). A simpler model that incorporated the observed diel states only (i.e., BiSSE-type model) performed much better than a model with the two hidden states only, supporting the stronger influence of diel activity patterns on speciation and extinction rates relative to the hidden state. Most importantly, for all trees and coding schemes, the full HiSSE model incorporating observed diel activity states (and hidden states) was much more strongly supported than the similarly complicated HiSSE Null4 model, which ignored diel activity (AICc difference between models ranged from 191 to 252 depending on the tree).

Using the full HiSSE model, the default root assumption (madfitz) had the strongest support, except for the Hackett tree with maximum diurnal coding (Table S2). All subsequent results are based on the best-fitting root assumption for that tree and coding method.

Under the full HiSSE model, diversification rates (speciation–extinction) were generally substantially higher in diurnal lineages than in nocturnal lineages (Table S3), by roughly 40%, based on summing values for both the observed and hidden states. In these cases, diurnal lineages have both higher speciation rates and higher extinction rates than nocturnal lineages, but still yielding higher diurnal diversification rates overall. In the case of the Ericson tree with maximum diurnal coding, the diurnal and nocturnal diversification rates are almost equal, with slightly higher diversification rates in nocturnal lineages. Estimated transition rates among states are summarized in Table S4.

Ancestral reconstructions (under the full HiSSE model) of the two diel activity states at each node using the best-fitting model for each tree and coding scheme are shown in Figures S1–S4. The results are summarized graphically in Figure 1, and verbally below. Statistical support for each state at key nodes is presented in Table S5.

Under most trees and coding methods, most of the major nodes within tetrapods are strongly supported as having been ancestrally nocturnal (Table S5), including the ancestors of tetrapods, amniotes, amphibians, mammals, diapsids (lepidosaurs, turtles, and archosaurs), lepidosaurs (lizards, snakes, tuatara), turtles, archosaurs (crocodylians and birds), and crocodylians. In contrast, the ancestor of birds is strongly supported as diurnal. With the Ericson tree and diurnal coding, a few of these ancestral nodes are not strongly supported but still show more support for a nocturnal ancestor (0.76–0.79) including diapsids, lepidosaurs, and archosaurs (Table S5). Using the nonoptimal assumption for root priors generally yielded similar results (Table S6). Specifically, almost all these nodes remain strongly

**Table 3.** Fit of different evolutionary models to the data on diel activity, given different trees (Ericson vs. Hackett) and different coding methods (four or two states with crepuscular and arrhythmic species coded as either diurnal [maximum diurnal coding] or nocturnal [maximum nocturnal coding]). Models are EL (estimated lambda) and WN (white noise). ML = maximum likelihood of model.

Tree	Coding	Model	ML	AICc
Ericson tree	Four-state	EL	-965.61	1957.42
	Four-state	WN	-1780.93	3567.87
Ericson tree	Maximum diurnal	EL	-701.60	1409.21
	Maximum diurnal	WN	-1304.01	2610.03
Ericson tree	Maximum nocturnal	EL	-590.33	1186.67
	Maximum nocturnal	WN	-1326.62	2655.24
Hackett tree	Four-state	EL	-964.09	1954.38
	Four-state	WN	-1780.93	3567.87
Hackett tree	Maximum diurnal	EL	-699.81	1405.63
	Maximum diurnal	WN	-1304.01	2610.03
Hackett tree	Maximum nocturnal	EL	-590.30	1186.61
	Maximum nocturnal	WN	-1326.62	2655.24

**Table 4.** Tests of phylogenetic signal in diel activity under different binary coding schemes and tree topologies, using the *D*-statistic.

	Estimated <i>D</i>	Probability of <i>D</i> different from Brownian motion (strong signal)	Probability of <i>D</i> different from random noise (no signal)
Maximum diurnal			
Ericson	0.01507	0.465	<0.001
Hackett	0.01220	0.468	<0.001
Maximum nocturnal			
Ericson	-0.10653	0.760	<0.001
Hackett	-0.12019	0.794	<0.001

Estimated *D* is scaled according to the data's similarity to *D* values of datasets simulated under models of Brownian motion (strong phylogenetic signal) and random noise (no phylogenetic signal). Smaller values provide stronger support for phylogenetic signal, with negative values suggesting that traits are highly conserved. Probabilities (*P* values) indicate whether the observed *D*-statistic is significantly different from 0 (Brownian motion) and from 1 (random noise).

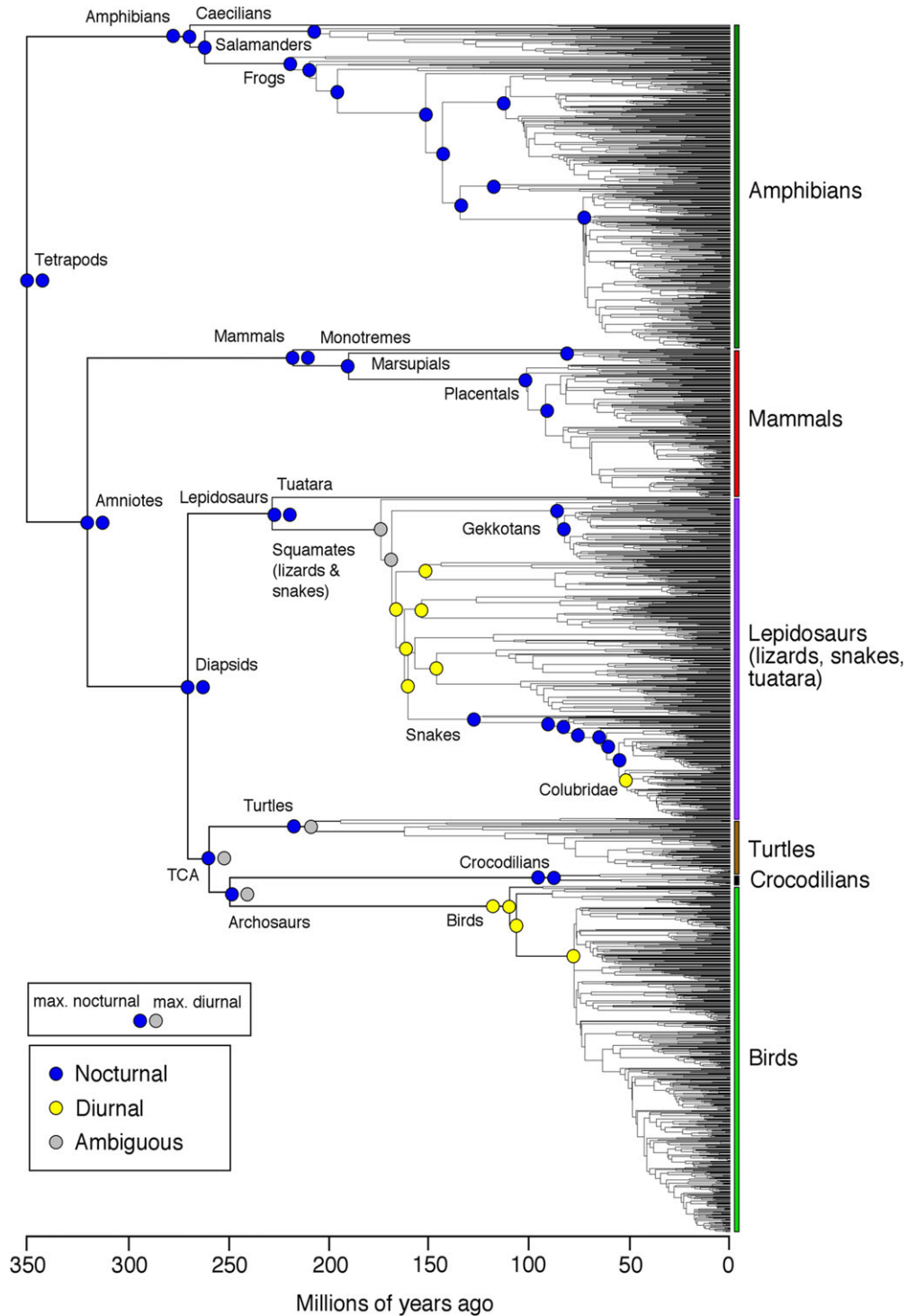
supported as ancestrally nocturnal, except for the root node in the Ericson tree under diurnal coding.

We also found many interesting transitions within these major groups (Figs. 1 and S1–S4). Many of these have been suggested before, but not necessarily demonstrated with an explicit phylogenetic analysis. For example, most ancestral nodes within amphibians were unambiguously reconstructed as nocturnal, but with several independent origins of diurnality in some frog clades, including South American poison-arrow frogs (Dendrobatidae), Madagascan mantellids, and some Brazilian stream-breeding frogs (Hylodidae). Similarly, most ancestral nodes within mammals were reconstructed as being nocturnal, but with many independent transitions to diurnality, including in artiodactyls, primates, elephants (and relatives), and several rodent clades. Most nodes within birds were reconstructed as diurnal, with independent origins of nocturnality in some groups, such as owls and caprimulgids. The ancestral state for squamates depended on the coding method and tree. The nocturnal tuatara (*Sphenodon*) is the sister group to squamates within Lepidosauria. Dibamids (with ar-

rhythmic activity) are the sister group to all other squamates in our tree, and above dibamids, the sister group to all other squamates are the predominantly nocturnal gekkotans. Within gekkotans, we found two major reversals to diurnality (in *Phelsuma* and *Lygodactylus* in Gekkonidae, and in Sphaerodactylidae; see Gamble et al. 2015 for a more extensive analysis). Most other nodes among lizard families were reconstructed as diurnal. Intriguingly, the ancestor of snakes (which is nested within lizards) was reconstructed as nocturnal, as were many basal nodes within snakes. There was then a major reversal to diurnality in the ancestor of the relatively derived, species-rich family Colubridae (but with considerable subsequent evolution within this clade), based on all analyses except for the Ericson tree with diurnal coding (which suggests the ancestor of Colubridae was nocturnal, Fig. S1).

Maximum-likelihood reconstructions using hidden rate classes but no differences in speciation and extinctions rates among states (corHMM; Table S7) generally supported two rate classes per diel state (but three for the Hackett tree with maximum diurnal coding). Comparison of different root state assumptions





**Figure 1.** Summary of reconstructed patterns of diel niche evolution for major nodes across tetrapods (using HiSSE). Blue and yellow circles indicate selected nodes that are reconstructed as being either nocturnal (blue) or diurnal (yellow). Two circles next to a node are the major clades for which statistical support was estimated (see Table S5 for details), summarizing results under maximum nocturnal (circle on left) or maximum diurnal (circle on right) coding. For these nodes, blue or yellow indicates that the mean proportional likelihood for that state was 0.88 or higher across both trees; gray indicates that the mean proportional likelihood was 0.87 or less for the most likely state across both trees. For nodes with a single circle, the results are summarized based on the best-supported state from HiSSE (see Figs. S1–S4 for details). This state is the same across trees and coding methods (except colubrid snakes, which are nocturnal under one tree and coding method). The tree shown includes 1914 species and is based on the backbone tree of Hackett et al. (2008) within birds (see Methods). The colored vertical bars indicate membership of species in named clades (e.g., dark green: amphibians; red: mammals).

supported the default madfitz assumption as having the best support (although AIC differences were often small; Table S8). Estimated transition rates under the best-fitting model for each tree and coding method are given in Table S9.

Reconstructions using corHMM and the best-fitting model for each tree and coding scheme strongly supported tetrapods, amphibians, amniotes, mammals, diapsids, archosaurs, and crocodylians as ancestrally nocturnal (Table S10; Figs. S5–S8). Turtles, lepidosaurs, and the clade of turtles, archosaurs, and birds were generally supported as nocturnal (but not always with strong support). Aves were either ambiguous or diurnal. Thus, the results from HiSSE and corHMM were generally highly concordant (although HiSSE models incorporating differences in speciation and extinction rates had better fit, and should therefore be considered the primary results). Reconstructions using corHMM with alternative (nonoptimal) assumptions for the root-state prior yielded broadly similar results (Tables S11–S12), with generally strong support for tetrapods as ancestrally nocturnal, but more variable support for most other nodes.

Finally, considering these reconstructions in light of the time-calibrated tree suggests a striking pattern of conservatism in this trait. Specifically, many nocturnal species of amphibians and mammals (and possibly other groups) seem to have retained this trait from a nocturnal common ancestor that lived approximately 350 million years ago (Figs. 1 and S1–S8).

This inference was generally supported by the stochastic mapping analyses, especially for the binary data (Table S13). The stochastic mappings of the two-state data (maximum diurnal, maximum nocturnal) across the different codings and trees show that the root is most often estimated to be nocturnal (60–88% of replicates). In replicates with a nocturnal root, that state is frequently retained continuously to the present day, in both amphibians and mammals (87–100%). Using the four-state data with all transition rates different between states led to different results. Even though the root was still frequently inferred to be nocturnal (76–96%), this state was not always retained continuously to the present day in amphibians and mammals, for the Hackett tree (only 58–74%) and especially the Ericson tree (0% of replicates). Instead, there were many very brief origins and losses of the intermediate states (crepuscular, arrhythmic), especially for the Ericson tree. This pattern seemed to occur because very high rates were estimated for these intermediate states (rate estimates in Table S14), seemingly related to the general problem of rare states for likelihood inference (Davis et al. 2013). Thus, these results appear to be artifactual. Indeed, the rate matrices for the two trees were very different for the four-state data (Table S14), and were actually uncorrelated ( $r = 0.061$ ;  $P = 0.8507$ ), despite the limited differences in topology (identical except within birds). Therefore, we also performed stochastic mapping using the much simpler equal rates model for the four-

state data. This model showed frequent estimation of nocturnality at the root (84–96%), more frequent retention of the nocturnal state to the present day (81–100%), and fewer transitory gains and losses of intermediate states. Again, we caution that all of these stochastic mapping analyses were based on simple models that were rejected for these data (i.e., they ignore rate heterogeneity and impacts of speciation and extinction rates). Nevertheless, they show that the nocturnal state could potentially be retained continuously from the tetrapod crown to the present day.

## Discussion

In this study, we analyzed patterns of diel niche evolution across terrestrial vertebrates. Our results showed strong, significant phylogenetic signal in this trait. We also found that tetrapods were most likely nocturnal ancestrally, and that many lineages that are nocturnal today have ancestors that appear to have maintained this trait continuously for at least 350 million years (e.g., amphibians, mammals). These patterns are particularly intriguing because of the demonstrated potential for lability of diel activity patterns within species (see Introduction), and because a majority of tetrapod species seem to be diurnal. Our results suggest that the greater number of diurnal species today may be related to higher rates of speciation and diversification in diurnal lineages.

More generally, our results show that traits involved in resource partitioning at the local scale can be conserved over surprisingly long-time scales. For example, in addition to the deep patterns inferred between these major clades, we also showed that diurnal activity was conserved across most lineages of birds for >100 Myr (million years) and for >150 Myr in lepidosaurs (Fig. 1; Table 1). Similarly, nocturnal activity appears to have been present and conserved among most species of amphibians for >250 Myr and for >150 Myr in mammals, and >100 Myr in snakes (Fig. 1; Table 1). This pattern of conservatism may also help explain why major shifts in diel activity among closely related species due to competition or predation seem to be rare (Kronfeld-Schor Dayan 2003). In other words, we show that much of the partitioning of the temporal niche among species and clades seen in present-day communities may have actually arisen tens or even hundreds of millions of years ago. This possibility was discussed for squamates by Vitt et al. (2003), but without explicit analyses.

Our results raise numerous questions for future research and have implications for several diverse research topics. First, why might diel activity niches be conserved over such long time-scales? One potential class of explanations is that different clades may be specialized for different abiotic conditions associated with different diel activity niches. For example, many amphibians are adapted to relatively cool and moist conditions (and have correspondingly low body temperatures; Vitt and Caldwell 2009),

and they may avoid desiccation and lethally high temperatures by being active at night. Conversely, some diurnal ectotherms may be constrained by the need for high temperatures that can only be achieved during the day, and dramatic physiological evolution may be required to switch between nocturnal and diurnal patterns (e.g., as demonstrated for geckoes; Autumn et al. 1999). Biological rhythms may themselves underlie long-term phylogenetic conservatism in this trait (Kronfeld-Schor and Dayan 2003). Similarly, visual systems may become specialized for a particular light regime, which may make it difficult for one species to see adequately in both environments and thereby reduce transitions between diel states (Kronfeld-Schor and Dayan 2003). Thus, the question of “why be conserved?” may be related to the question of “why be specialized?” There may also be competitive effects, limiting invasion of occupied diel niches (as postulated between early, nocturnal mammals and diurnal, nonavian dinosaurs; review in Gerkema et al. 2013). At the same time, despite the overall pattern of long-term conservatism, there are also many transitions within many groups (e.g., many independent origins of diurnality in frogs and mammals; Figs. S1–S4). Some of these could be quite rapid. Understanding why transitions occur in some groups and not others may be particularly revealing for understanding the causes of both conservatism and diel niche shifts. Finally, we emphasize that our analyses address shifts between overall day versus night activity patterns, and do not address temporal activity patterns within these broad categories, which might be considerably more labile.

Our results also suggest that lineages of strictly diurnal species have higher rates of speciation and overall diversification (speciation – extinction) than nocturnal species (maximum nocturnal coding in Table S3). This may explain why the major diurnal tetrapod lineages appear to be relatively young in our tree (e.g., ~100 Ma in birds; ~160 Ma in squamates; Fig. 1), but are collectively more species rich than nocturnal lineages (Table 1). It may be that major groups of diurnal tetrapods (e.g., in non-avian dinosaurs and synapsids; Schmitz and Motani 2011; Angielczyk and Schmitz 2014) have gone extinct and been replaced more recently by nocturnal lineages that have invaded and rapidly diversified in the diurnal niche, consistent with our results showing that strictly diurnal lineages also seem to have much higher extinction rates (Table S3). The causes of these differences in diversification rates could be an intriguing area for future research. However, we caution that it remains uncertain if and how diel activity directly affects diversification.

The potential impact of diel activity patterns on diversification might also be relevant to patterns of species richness among tetrapod clades. For example, the higher speciation rates of diurnal lineages may help explain why the largely diurnal squamates and birds are more species rich than the predominantly nocturnal amphibians, mammals, and crocodylians (Table 1), and despite

the older ages of amphibians and mammals (Fig. 1; for both stem and crown-group ages), and thus more time for species richness to accumulate in these clades. Overall, the ecological factors that underlie diversification and richness patterns among major tetrapod clades remain surprisingly underexplored (but see Wiens 2015a).

Large-scale patterns of diel activity evolution may also have important implications for diet. Intriguingly, true herbivory (i.e., subsisting mostly on leaves, not just fruit or seeds) seems to be rare among nocturnal lineages. To our knowledge, there are effectively no herbivorous (adult) amphibians, snakes, or crocodylians (which are predominantly nocturnal clades), and herbivory appears to be largely absent among nocturnal lepidosaurs and turtles (Vitt and Caldwell 2009). This pattern may occur because true herbivory requires gut endosymbionts that need relatively high host body temperatures to function (Zimmerman and Tracy 1989; Vitt and Caldwell 2009), and these high temperatures may be difficult to maintain in nocturnal ectothermic lineages. Furthermore, many of the major herbivorous lineages of mammals are primarily diurnal (e.g., elephants, artiodactyls; Pough et al. 2009; Figs. S1–S4). Some forms of herbivory are common in birds (Pough et al. 2009), and birds are predominantly diurnal (Table 1). It may be that patterns of diel activity drive large-scale patterns of diet evolution (or vice versa) and this potential association should be tested in future studies.

There may also be important implications of diel niche evolution for the evolution of communication and sensory systems. For example, visual communication systems may evolve more often in diurnal lineages (e.g., bright plumages in birds), whereas acoustic communication (and chemical communication) may evolve more often in nocturnal lineages (e.g., vocalizations in frogs, crocodylians, and geckoes; Pough et al. 2009; Vitt and Caldwell 2009), as suggested by Kronfeld-Schor and Dayan (2003). In some ways, birds may appear to be an obvious exception (primarily diurnal but utilizing acoustic communication as well as visual; Pough et al. 2009). However, acoustic communication is also present in crocodylians (Pough et al. 2009; Vitt and Caldwell 2009), and so presumably evolved in a shared ancestor of birds and crocodylians (which may have been nocturnal; Fig. 1). It may be that the antecedents of bird song originated in nocturnal ancestors, and this nocturnal origin may be involved in the enigmatic tendency for many diurnal birds to call more extensively at dawn instead of during daylight hours (e.g., Berg et al. 2006). Again, these patterns will need to be tested with focused studies in the future.

In this study, we included a simple approach for quantifying niche conservatism that has been largely neglected in the recent literature (but see Wiens 2015b): the greatest absolute amount of time that a trait has been maintained continuously in a given clade (e.g., tetrapods). We refer to this as the “trait retention index.” Specifically, this is the time between the oldest origin of the state in a given time-calibrated tree and its continuous presence to the

present day in a given lineage, based on ancestral-state reconstructions at each node. Note that this approach does not require that every species in a clade share the same state, but instead requires an unbroken chain of unambiguous reconstructions of the same state, from an extant species to the oldest node in the chain where the state appears. Many other tests for niche conservatism have been proposed and used (e.g., Wiens et al. 2010), but most ignore the absolute timescale over which traits are conserved (such as those comparing the fit of different evolutionary models, Tables 2 and 3). Although this approach is a quantitative descriptor rather than a statistical test per se, it provides an index that can readily be compared across taxa and traits.

Our results also provide a striking counterexample to the common (if implicit) view that ancestral state reconstructions necessarily become more ambiguous at deeper phylogenetic scales. We find that many reconstructions of diel activity have strong statistical support, including nodes that are 350 Myr old (i.e., tetrapods; Fig. 1). Instead, ambiguity may be more likely to be explained by patterns of variability among species in a clade rather than the absolute age of the clade itself. Of course, just because reconstructions are statistically unambiguous does not mean that they are correct. However, our reconstructions from some key nodes have support from other lines of evidence. For example, detailed analyses of eye morphology in fossil synapsids suggest that nocturnality was the ancestral state in the lineage leading up to mammals, long before the origin of crown-group mammals (Angielczyk and Schmitz 2014), consistent with our results. Eye shape morphology also supports the idea that mammals were ancestrally nocturnal (i.e., large cornea relative to eye size; Hall et al. 2012). Analyses of scleral ring morphology support ancient nocturnality in (at least some) dinosaurs (Schmitz and Montani 2011), consistent with our results suggesting that archosaurs were ancestrally nocturnal (although our results are also consistent with the idea that diurnality evolved within dinosaurs, after the origin of stem archosaurs and before the origin of crown birds). Similar morphological analyses could provide further testing of the patterns based on ancestral reconstruction found here. Analyses of visual systems (and their genes) in living taxa may also provide important insights. For example, many authors have discussed the absence of the visual pigments RH2 and SWS2 in mammals as evidence that they were ancestrally nocturnal, and some authors have suggested that there was independent loss of RH2 in the ancestor of amphibians, which also lack this pigment (e.g., Bowmaker 2008; Gerkema et al. 2013). These inferences are consistent with our results showing each of these two groups as ancestrally nocturnal. Furthermore, given the phylogenetic relationships of these taxa, this pattern is also consistent with the absence of this pigment in the ancestors of tetrapods and of amniotes, which we infer here as nocturnal (rather than independent loss in amphibians and mammals). Chang et al. (2002) inferred the sequence of

the rhodopsin gene in the ancestor of archosaurs, and then synthesized this gene in the laboratory and tested its function. Based on their results, they suggested that this ancestor may have been nocturnal, as inferred here. However, we caution again that these supporting inferences are relatively indirect (assuming a relationship between morphology and diel activity or visual pigments and diel activity, as opposed to making inferences based directly on observed diel activity patterns), are often based on very limited taxon sampling (especially for visual pigments), and most are not based on explicit model-based reconstruction methods (but see Chang et al. 2002). In summary, we note that just because a node is relatively old does not automatically make the estimated state for that node ambiguous or incorrect, and our reconstructions for some of the most ancient nodes are also supported by other (less direct) lines of evidence.

## Conclusions

In this study, we analyze the large-scale patterns of diel activity among tetrapod species. Our results show that diel activity patterns are phylogenetically conserved. They also suggest an intriguing pattern in which tetrapods were ancestrally nocturnal and gave rise to more recent diurnal lineages, which then diversified more rapidly to yield the large number of diurnal species seen today. Overall, these results may have implications for many other areas, such as community ecology, the evolution of diet and communication systems, and patterns of species richness. They also demonstrate a potentially widely applicable measure of niche conservatism. Data are available on Dryad (<https://doi.org/10.5061/dryad.fg700>).

## AUTHOR CONTRIBUTIONS

SRA and JJW designed the study, SRA and JJW performed analyses, and SRA and JJW wrote the paper.

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## DATA ARCHIVING

The doi for our data is <http://doi.org/10.5061/dryad.fg700>.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's website:

- Figure S1.** Maximum-likelihood ancestral-state reconstructions done using HiSSE (version 1.8, Beaulieu and O'Meara 2016), the backbone tree of Ericson et al. (2006) for birds, and the maximum diurnal coding scheme in which crepuscular and arrhythmic species are coded as diurnal.
- Figure S2.** Maximum-likelihood ancestral-state reconstructions done using HiSSE (version 1.8, Beaulieu and O'Meara 2016), the backbone tree of Hackett et al. (2008) for birds, and the maximum diurnal coding scheme in which crepuscular and arrhythmic species are coded as diurnal.
- Figure S3.** Maximum-likelihood ancestral-state reconstructions done using HiSSE (version 1.8, Beaulieu and O'Meara 2016), the backbone tree of Ericson et al. (2006) for birds, and the maximum nocturnal coding scheme in which crepuscular and arrhythmic species are coded as nocturnal.
- Figure S4.** Maximum-likelihood ancestral-state reconstructions done using HiSSE (version 1.8, Beaulieu and O'Meara 2016), the backbone tree of Hackett et al. (2008) for birds, and the maximum nocturnal coding scheme in which crepuscular and arrhythmic species are coded as nocturnal.
- Figure S5.** Maximum-likelihood ancestral-state reconstructions done using the corHMM package (version 1.20, Beaulieu et al. 2013), the backbone tree of Ericson et al. (2006) for birds, and the maximum diurnal coding scheme in which crepuscular and arrhythmic species are coded as diurnal.
- Figure S6.** Maximum-likelihood ancestral-state reconstructions done using the corHMM package (version 1.20, Beaulieu et al. 2013), the backbone tree of Hackett et al. (2008) for birds, and the maximum diurnal coding scheme in which crepuscular and arrhythmic species are coded as diurnal.
- Figure S7.** Maximum-likelihood ancestral-state reconstructions done using the corHMM package (version 1.20, Beaulieu et al. 2013), the backbone tree of Ericson et al. (2006) for birds, and the maximum nocturnal coding scheme in which crepuscular and arrhythmic species are coded as nocturnal.
- Figure S8.** Maximum-likelihood ancestral-state reconstructions done using the corHMM package (version 1.20, Beaulieu et al. 2013), the backbone tree of Hackett et al. (2008) for birds, and the maximum nocturnal coding scheme in which crepuscular and arrhythmic species are coded as nocturnal.
- Figure S9.** Stochastic mapping results (25 replicates) using maximum diurnal coding and the Ericson tree.
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- Supplementary File 1.** Phylogeny of 1914 tetrapod species used in this study, based on the Ericson tree for birds.
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- Supplementary File 6.** R scripts used in *geiger* and *caper* analyses.
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- Supplementary File 12.** Datafile used in *phytools* analyses with maximum diurnal coding.
- Supplementary File 13.** Datafile used in *phytools* analyses with maximum diurnal coding.
- Table S1.** Comparison of fit of different HiSSE models for binary coding of diel activity states, under different trees (Ericson and Hackett backbone for birds) and coding approaches (maximum diurnal and maximum nocturnal).

**Table S2.** Comparison of fit of different root state prior assumptions, using full HiSSE models and binary coding of diel activity states, for both trees (Ericson and Hackett backbone for birds) and coding approaches (maximum diurnal and maximum nocturnal).

**Table S3.** Estimated parameters for the diurnal character state (0) and nocturnal state (1) as well as two hidden states (A and B), using a full HiSSE model including the best-fitting root prior assumption (either “madfitz” or “equal,” see Table S2).

**Table S4.** Matrices of the estimated transition-rate parameters for each tree (Ericson and Hackett backbones) and coding scheme (maximum diurnal and maximum nocturnal) constructed using the best-fitting root prior assumptions (either “madfitz” or “equal,” see Table S2).

**Table S5.** Reconstructed diel activity states at key nodes of tetrapod phylogeny based on full HiSSE models and best-fitting root-prior assumptions.

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**Table S7.** Comparison of the fit of different corHMM models differing in the number of hidden rate classes, using binary coding of diel activity states.

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**Table S9.** Matrices of the estimated transition-rate parameters for each tree (Ericson and Hackett backbones) and coding scheme (maximum diurnal and maximum nocturnal) under the best-fitting root prior assumption (madfitz).

**Table S10.** Reconstructed diel activity states at key nodes of tetrapod phylogeny based on corHMM models and the optimal “madfitz” assumption for the root-state prior.

**Table S11.** Reconstructed diel activity states at key nodes of tetrapod phylogeny based on corHMM models and the suboptimal “yang” assumption for the root-state prior.

**Table S12.** Reconstructed diel activity states at key nodes of tetrapod phylogeny based on corHMM models and the suboptimal “null” assumption for the root-state prior.

**Table S13.** Summary of stochastic mapping results, showing the percentage of 25 replicates in which one or more amphibian species and mammal species have retained nocturnal activity from the tetrapod root, without passing through another state.

**Table S14.** Matrices of the estimated transition rate parameters for the stochastic mapping analyses.