

Historical Contingency and Animal Diets: The Origins of Egg Eating in Snakes

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Submitted June 19, 2005; Accepted January 20, 2006;

Electronically published April 5, 2006

Online enhancements: appendices.

ABSTRACT: Evolutionary changes in animal diets must often begin through the inclusion of a novel food type as a minor component of the diet. An aspect of this initial change that has rarely been studied is the relationship between the existing diet and the use of specific novel foods. We used comparative analyses to test the hypothesis that, in snakes, feeding on squamate (lizard and snake) eggs or bird eggs—items that represent evolutionarily derived and, in most cases, minor components of the diet—is associated with feeding on squamates or birds, respectively. Phylogenetic concentrated-changes tests indicate a significant tendency for predation on eggs to arise in snake lineages characterized by feeding on the corresponding animals. These results also generally hold for analyses including only snake species that are likely to encounter eggs and are large enough to ingest them. The inferred histories of specialized egg eaters also support the hypothesis. Because snakes often use chemical cues to recognize prey, the observed phylogenetic patterns might be explained by chemical similarities between eggs and adult animals. Our results suggest broad effects of predispositions on snake diets and thus illustrate how historical contingencies can shape the ecology of organisms.

Keywords: chemical cues, contingency, dietary evolution, egg eating, predisposition, snakes.

Striking adaptations to different diets are an obvious aspect of the evolutionary diversification of animals (e.g., Kamil et al. 1987; Rosenthal and Berenbaum 1991; Schwenk 2000; Eisner 2003). Shifts in diet presumably often begin through

the incorporation of some novel food type as a minor component of the diet. This initial stage in the evolution of a new feeding habit has received relatively little attention, perhaps because, almost by definition, it is not associated with striking phenotypic changes. However, the initial incorporation of novel foods is a critical step in determining the overall course of the evolution of feeding habits and, in addition, has an immediate influence on patterns of resource use.

An obvious starting point for the study of this initial stage of a dietary shift is to determine whether species with certain existing diets are especially likely to begin feeding on particular novel foods. There are two general reasons to expect such relationships. The first is correlated occurrence: a novel food is more likely to be encountered if its density is correlated with that of some typical food of the animal. For example, a herbivore that feeds on sagebrush and chooses habitats with a high density of these plants will have the opportunity to include sagebrush-associated plants in its diet. The second is specific feeding predispositions: traits that facilitate feeding on some typical food of the animals in question might also facilitate feeding on the novel food. These traits might act at any stage in the procuring or processing of food (e.g., in the stages of searching, recognition, ingestion, or digestion). A well-known example of this phenomenon is the attraction of many phytophagous insects to novel plants that share distinctive secondary compounds with the insects' typical host plants (Thorsteinson 1960; Ehrlich and Raven 1964; Rosenthal and Berenbaum 1991).

In this study, we focus on the incorporation of squamate (lizard and snake) eggs and bird eggs into the diets of snakes. Some snake species are specialist feeders on such eggs; members of the genus *Dasypeltis* (African egg-eating snakes), which apparently feed only on bird eggs and have evolved a suite of morphological adaptations for ingesting eggs (Gans 1952, 1974), are the best-known example. In addition, many other snake species eat squamate eggs and/or bird eggs at least occasionally.

We hypothesize that egg eating is especially likely to arise in snake species that already feed on the animals that

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lay the eggs (hereafter referred to as the “corresponding animals”); for example, feeding on squamate eggs is most likely to occur in snakes that already feed on squamates. There are at least two reasons to expect this pattern. The first falls into the category of correlated occurrence. Specifically, the density of breeding squamates and birds in an area should be highly and positively correlated with the density of squamate eggs and bird eggs. This correlation could produce a positive association between feeding on eggs and feeding on the corresponding animals.

The second and more novel explanation for an association between feeding on squamates or birds and feeding on the eggs of these animals is based on a possible chemical similarity between these two kinds of food. Most snakes use chemical cues in some stage of prey recognition (Burghardt 1990; Ford and Burghardt 1993; Schwenk 1994). This raises the possibility that snakes that eat squamates or birds may also recognize the corresponding eggs as suitable food because of some similarity in the chemical “signatures” of eggs and adults. Such a chemically mediated predisposition for feeding on eggs would be analogous to a predisposition in insects for feeding on a novel host plant that shares a key secondary compound with the insects’ typical hosts. This explanation falls into the category of specific feeding predispositions.

Here we use comparative methods applied to data compiled from the literature on snake diets to statistically evaluate the possible association between feeding on eggs and feeding on the corresponding animals. Specifically, we test these two predictions: the habit of eating squamate eggs tends to arise coincident with or subsequent to the habit of feeding on squamates (the “squamate-first prediction”); and the habit of eating bird eggs tends to arise coincident with or subsequent to the habit of feeding on birds (the “bird-first prediction”). These statistical analyses primarily concern snakes that eat eggs but are not specialist egg eaters. In addition, we attempt to infer whether specialist egg eaters have arisen from ancestors that ate the corresponding animals. Our results suggest that organismal predispositions that differ among snake lineages are likely important factors in determining how often and in what taxa the habit of egg eating has arisen.

Methods

Diet, Lifestyle, and Body Size Compilations

We surveyed the literature through summer 2002 for studies that reported quantitative data on snake diets. Data from A. de Queiroz’s unpublished studies of *Thamnophis* (North American garter snakes) were also included. We took care to account for redundancy among dietary records (e.g., Fitch 1982, 1999). We included only species for

which the total sample size (number of prey items or, if this was not reported, number of snakes containing prey) was at least 20. We restricted the study to Alethinophidia, which is one of the two clades resulting from the basal split in crown-group snakes and includes more than 85% of all described snake species. Members of the other main clade, Scolecophidia (blind snakes and thread snakes), were excluded because none of them are known to eat any of the relevant food items (i.e., squamates, squamate eggs, birds, and bird eggs; see the next subsection for further explanation). The total number of species in the data set was 200 (app. A in the online edition of the *American Naturalist*).

We categorized the general habit (terrestrial, aquatic, arboreal) of each snake species from literature accounts, primarily in field guides and other works on regional snake faunas, and our own observations of many of the included species. A species was considered aquatic or arboreal only if its members are thought to feed primarily in the water or above the ground in vegetation, respectively. Habit categories were chosen because of an expected relationship to egg eating that we wanted to take into account (see next subsection). In particular, aquatic snakes probably encounter squamate eggs and bird eggs less frequently than do other species, and arboreal snakes probably encounter bird eggs more frequently and squamate eggs less frequently than do terrestrial species. We pooled the few semi-fossorial snakes in the data set with terrestrial snakes.

Snake body size may be an important variable because snakes typically swallow prey whole, and thus, maximum prey size is a function of snake gape size. We used maximum reported total length as the measure of snake body size because this was the only size measure available for all species in the data set. Body size data were taken from the literature, primarily from the compilation of Boback and Guyer (2003) and from field guides and other works on regional snake faunas. The full data set, with dietary and body size references, is given in appendix A.

Concentrated-Changes Tests

Preliminary nonphylogenetic analyses using species as data points suggested that egg eating should be treated as a discrete rather than a continuous variable. Specifically, logistic regressions using the presence/absence of squamate eggs or bird eggs in the diet as dependent variables and multiple independent variables (presence/absence of the corresponding animals in the diet, snake habit, total number of prey, maximum snake length, and snake taxon [viperid or nonviperid]) explained more of the variance than standard regressions using the proportion of squamate eggs or bird eggs in the diet as dependent variables (results not shown). An appropriate test for evaluating our pre-

dictions with egg eating coded as a discrete character is Maddison's (1990) concentrated-changes test. This test determines whether origins of a trait are significantly more likely to occur on branches of the phylogeny characterized by some other trait than one would expect if these origins were distributed randomly on the tree. In this study, we wanted to determine whether origins of egg eating are especially likely to occur on branches characterized by the habit of eating the corresponding animals. We used MacClade 4.03 (Maddison and Maddison 2001) to implement the test.

We performed initial concentrated-changes tests using all taxa. To help infer whether significant patterns observed can be attributed to factors other than general habit or body size, we performed additional analyses excluding taxa with habits or body sizes that should result in a very low probability of eating eggs. For the bird-first case, a second set of analyses excluded all aquatic species (none of which ate bird eggs) and all species smaller than the smallest species in our sample that ate birds. A third set of analyses for the bird-first case excluded all aquatic species and all species smaller than the smallest species in our sample that ate bird eggs. This third set is probably excessively conservative because the smallest species that ate bird eggs was quite large (*Lampropeltis calligaster* [yellow-bellied king snake]; maximum reported total length of 143 cm), and therefore these analyses excluded many species that are large enough to eat bird eggs. The second and third sets of analyses were also repeated with viperids (vipers and pit vipers) excluded because no viperid ate bird eggs. For the squamate-first case, a second set of analyses excluded both aquatic and arboreal species (none of which ate squamate eggs) and all species smaller than the smallest species in our sample that ate squamate eggs. We did not perform analyses excluding all species smaller than the smallest species that ate squamates because such analyses would have been very similar to the set just described.

For each test, 10,000 simulated histories of the evolution of egg eating were performed to obtain a null distribution for the number of origins of egg eating occurring on branches characterized by the habit of eating the corresponding animals. The ancestral state in these simulations was assumed to be lack of egg eating because this was the ancestral state in all the observed reconstructions. In the simulations, we used the number of origins of egg eating inferred by parsimony rather than the actual number of origins because the "observed" number of origins for the original data also was inferred by parsimony. Character state reconstructions are likely to be less accurate when fewer taxa are included. Thus, in the analyses excluding some taxa, we fixed the states of the independent variables (presence/absence of birds/squamates in the diet) at all

nodes of the tree to match the reconstructions obtained when all taxa were included.

We performed concentrated-changes tests using both the minimum state (MINST) and maximum state (MAXST) character reconstruction options for the dependent variables. For our purposes, MAXST is conservative because it reduces the number of origins of egg eating, compared to MINST. We used MINST and MAXST rather than the more familiar delayed-transformation (DELTRAN) and accelerated-transformation (ACCTRAN) options because the concentrated-changes test in MacClade does not allow the use of DELTRAN and ACCTRAN for the dependent variable. For the reconstructions of the independent variables, we used both DELTRAN and ACCTRAN options. In our analyses, DELTRAN gave more conservative results in some cases, ACCTRAN in others.

The concentrated-changes test implicitly assumes that the focal independent character (here, presence/absence of eating the egg-laying animals) is the only character that can affect the probability of origin of the dependent character state of interest (egg eating; Read and Nee 1995). If this assumption holds, simulations suggest that the test is generally conservative (Lorch and Eadie 1999). However, the assumption probably is violated in most real cases. A particular problem arises if many of the included taxa have inherited a state of a third character (or of multiple characters) that precludes or greatly reduces the probability of origin of both focal states of interest (feeding on the egg-laying animals and on their eggs). In that case, the evidence against the null hypothesis will be inflated (Maddison 1990; Sillén-Tullberg 1993; Read and Nee 1995). It was for this reason that we excluded scolecophidian snakes from the analyses. Scolecophidians are all narrow-headed, strongly fossorial snakes specialized for feeding on soft-bodied invertebrates (Greene 1997); that is, they have inherited traits that greatly reduce the likelihood of feeding on vertebrates or their eggs. In addition, the analyses restricted to species with certain habits and above a certain body size eliminate other taxa that should have low probabilities of feeding on some of the focal food types, although the feeding restrictions in these cases are probably less strong than those for the scolecophidians. The above considerations emphasize that the restricted analyses provide the strongest test for a direct, causal relationship between eating eggs and eating the corresponding animals (although we do not claim that these analyses have circumvented all limitations of the concentrated-changes test).

We also tested our hypotheses through estimation of stochastic models of character evolution in a Bayesian framework, using the program Reversible Jump (RJ)-Discrete (Pagel and Meade 2006). With the default options (equal branch lengths, no variation in character change

rates among branches), these analyses agreed with the concentrated-changes results reported below. However, the RJ-Discrete runs often visited models that included unrealistically high rates of character change. Thus, we think that the concentrated-changes test is more appropriate for our data.

Construction of the Snake Supertree

To implement the concentrated-changes tests, we constructed a phylogeny of all included species, using trees from numerous phylogenetic studies (a “supertree”; Sanderson et al. 1998). We began with relationships among major lineages of snakes and placed successively less inclusive groups within this growing tree, as in the construction of a phylogeny of flowering plants by Webb and Donoghue (2001). For example, once relationships among major snake lineages were assembled, the tree representing relationships among families and subfamilies of Colubroidea was placed within this larger framework. Our basic strategy was to use the best available phylogenetic estimate at each hierarchical level rather than to use all available studies.

We used the following criteria to build the snake supertree. Maximum likelihood trees were preferred over trees obtained using other methods. Strict-consensus trees were used whenever possible. For a given clade, we chose trees based on the number of informative characters and the number of taxa. For example, if two trees (from the same study or, more typically, from different studies) were generated using similar numbers of characters, we selected the one with more taxa. In some cases, we used one study for most relationships in a clade but relied on other studies to place taxa that were not included in the first study. Monophyly of genera was assumed unless there was evidence against it. In a few cases, clade support measures influenced our choice of trees. For example, as an estimate of relationships among major lineages, we used the phylogeny of Lee and Scanlon (2002) rather than that of Vidal and Hedges (2002*b*) because the former had higher nodal support than the latter. Importantly, relationships that remained ambiguous were resolved in such a way that the number of origins of egg eating was minimized, which made the results of the analyses conservative. The supertree and additional details regarding its construction are given in appendix B in the online edition of the *American Naturalist*.

Histories of Specialist Egg Eaters

We considered a taxon (a species or genus) to be composed of egg-eating specialists if it met either of the following criteria: first, in our diet compilation, bird eggs or squa-

mate eggs made up more than half the diet of the species; second, anecdotal evidence suggests that eggs make up more than half the diet for the species in question (or for most species in the genus in question), and members of the taxon have morphological traits thought to be adaptations for egg eating. Four species met the first criterion: *Cemophora coccinea* (scarlet snake; 0.77 of the diet consisted of squamate eggs), *Simoselaps semifasciatus* (half-girdled snake; 1.0 squamate eggs), *Pantherophis vulpinus* (fox snake; 0.61 bird eggs), and *Pituophis melanoleucus* (pine snake; 0.57 bird eggs). Seven taxa met the second criterion (supporting references are indicated), but for only five of these could we make an inference about the origins of egg eating as described below: *Oligodon* (Kukri snakes; Minton and Anderson 1963; Broadley 1979; Toriba 1987; Coleman et al. 1993); *Phyllorhynchus* (leaf-nosed snakes; Klauber 1935; Bogert and Oliver 1945; Gardner and Mendelson 2003); *Stegonotus* (ground snakes; McDowell 1972); *Prosymna* (shovel-snout snakes; Broadley 1979); and *Dasypeltis* (Gans 1952, 1974).

We used two approaches to infer whether specialist egg eaters arose from snakes that ate the corresponding animals. For the four egg-eating specialists included in our diet data set, we used parsimony mapping of dietary characters (presence/absence of eggs and the corresponding animals) on our snake supertree to make this inference. In two other cases (*Prosymna* and *Dasypeltis*), available dietary and phylogenetic evidence allowed a similar character mapping, although the dietary evidence in these cases was sparser than for the previous four. In the remaining cases, lack of phylogenetic information precluded explicit character mapping. However, under the hypothesis that egg eating evolves from feeding on the corresponding animals, one would expect that some egg specialists occasionally feed on these animals. We noted whether this was observed.

Results

Concentrated-Changes Tests

The tendency for the habit of eating squamate eggs to arise on branches characterized by eating squamates is significant in all but one of the permutations (table 1). In the one exception, the result is close to significant ($P = .058$; table 1).

When all taxa are included or when aquatic species and species smaller than the smallest species that ate birds are excluded, the tendency for the habit of eating bird eggs to arise on branches characterized by eating birds is highly significant ($P < .01$) in all permutations (table 2). When aquatic species and species smaller than the smallest species that ate bird eggs are excluded, the tendency is sig-

Table 1: Concentrated-changes tests for an association between eating squamate eggs and eating squamates

Analysis ^a	Number of taxa	Origins for/against ^b	<i>P</i>	Origins after/same ^c
Alltaxa/MINST/DELTRAN	200	27/0	.0002	27/0
Alltaxa/MAXST/DELTRAN	200	19/0	.0137	18/1
Alltaxa/MINST/ACCTTRAN	200	27/0	<.0001	27/0
Alltaxa/MAXST/ACCTTRAN	200	19/0	.0044	18/1
Reduced/MINST/DELTRAN	147	25/0	.0206	25/0
Reduced/MAXST/DELTRAN	147	19/0	.0577	18/1
Reduced/MINST/ACCTTRAN	147	25/0	.0105	25/0
Reduced/MAXST/ACCTTRAN	147	19/0	.0282	18/1

^a "Alltaxa" includes all species except the two for which evidence of feeding on squamate eggs was ambiguous. "Reduced" additionally excludes aquatic snakes, arboreal snakes, and species smaller than the smallest species that ate squamate eggs. MINST and MAXST ("minimum state" and "maximum state," respectively) refer to options for choosing among equally parsimonious reconstructions of eating squamate eggs. DELTRAN and ACCTTRAN ("delayed transformation" and "accelerated transformation," respectively) refer to options for choosing among equally parsimonious reconstructions of eating squamates.

^b "Origins for/against," respectively, are origins of feeding on squamate eggs that occurred on branches characterized by feeding on squamates and those that occurred on branches not characterized by feeding on squamates.

^c "Origins after/same," respectively, are origins of feeding on squamate eggs that occurred after the corresponding origin of feeding on squamates and those that occurred on the same branch as the corresponding origin of feeding on squamates.

nificant when egg eating is reconstructed using MINST but not when using MAXST (table 2). The analyses excluding viperids gave very similar results (not shown).

The concentrated-changes test does not distinguish between cases in which feeding on eggs arises after feeding on the corresponding animals and those in which the two arise on the same branch. However, for most permutations, the majority of origins of egg eating that support our predictions are of the former kind (tables 1, 2).

Histories of Specialist Egg Eaters

Parsimony reconstructions indicate that the four species that our diet data set showed were egg specialists arose from snakes that ate the corresponding animals. Specifically, in all four cases, the most recent common ancestor

of the species in question and its sister group is inferred to have fed on the corresponding animals (fig. 1).

A phylogenetic analysis that includes the squamate-egg specialist *Prosymna* (Nagy et al. 2003), in conjunction with higher-level analyses of snake phylogeny (Vidal and Hedges 2002a; Kelly et al. 2003) and descriptions of diets of related taxa (Shine 1991a; Spawls et al. 2002), indicates that the immediate ancestor of *Prosymna* fed on squamates. Similarly, phylogenetic work on the bird-egg specialist *Dasyveltis* and its close relatives (R. Lawson, unpublished data), along with dietary data for these relatives (Savidge 1988; Greene 1989; Luiselli et al. 1998), strongly indicates that the most recent common ancestor of *Dasyveltis* and its sister group fed heavily on birds.

At least some members of the squamate-egg specialist genera *Oligodon*, *Phyllorhynchus*, and *Stegonotus* also feed

Table 2: Concentrated-changes tests for an association between eating bird eggs and eating birds

Analysis	Number of taxa	Origins for/against	<i>P</i>	Origins after/same
Alltaxa/MINST/DELTRAN	198	11/1	<.0001	8/3
Alltaxa/MAXST/DELTRAN	198	8/2	.0002	7/1
Alltaxa/MINST/ACCTTRAN	198	11/1	<.0001	10/1
Alltaxa/MAXST/ACCTTRAN	198	9/1	<.0001	7/2
Reduced1/MINST/DELTRAN	147	11/1	.0003	8/3
Reduced1/MAXST/DELTRAN	147	8/2	.0056	7/1
Reduced1/MINST/ACCTTRAN	147	11/1	.0001	10/1
Reduced1/MAXST/ACCTTRAN	147	9/1	.0013	7/2
Reduced2/MINST/DELTRAN	54	10/1	.0203	6/4
Reduced2/MAXST/DELTRAN	54	4/3	.5005	2/2
Reduced2/MINST/ACCTTRAN	54	10/1	.0463	8/2
Reduced2/MAXST/ACCTTRAN	54	6/1	.1068	3/3

Note: Terminology is the same as in table 1 (but replacing squamates and squamate eggs with birds and bird eggs), except as follows: "Alltaxa" includes all species except the five for which evidence for feeding on bird eggs was ambiguous. "Reduced1" additionally excludes aquatic snakes and species smaller than the smallest species that ate birds. "Reduced2" additionally excludes aquatic snakes and species smaller than the smallest species that ate bird eggs.

on adult squamates (*Oligodon*: Minton and Anderson 1963; Broadley 1979; *Phyllorhynchus*: Klauber 1935; Dial et al. 1989; *Stegonotus*: McDowell 1972; Shine 1991b), suggesting origins of egg eating from ancestors that ate squamates. However, the records for *Oligodon* are from observations of captive snakes.

Discussion

Support for the Squamate-First and Bird-First Predictions

The concentrated-changes tests using all taxa or the moderately reduced data sets support both the squamate-first and bird-first predictions. The habits of eating squamate eggs or bird eggs arise on branches characterized by feeding on the corresponding animals significantly more often than expected by chance (tables 1, 2), except for a marginally significant result in one permutation of the squamate data set. Of the four permutations of the strongly reduced bird data set, only two give a significant result, but, as noted above, these analyses are probably overly conservative because they exclude many taxa that are large enough to eat bird eggs.

The phylogenetic histories of specialist egg eaters also generally support our predictions. Character mapping indicates that all four egg specialists included in our diet data set had immediate ancestors that fed on the corresponding animals (fig. 1). The two other specialized egg-eating taxa (*Dasyveltis* and *Prosymna*) for which we could perform explicit character mapping show the same pattern. The bird-egg specialist group *Dasyveltis* is an especially striking case. Although few snake species feed substantially on birds (app. A), phylogenetic work in progress (R. Lawson, unpublished data) strongly indicates that *Dasyveltis* arose from immediate ancestors that fed heavily on birds. The squamate-egg specialists *Oligodon*, *Phyllorhynchus*, and *Stegonotus* also support our predictions in that they occasionally eat adult squamates.

Our data set undoubtedly underestimates the number of species that occasionally feed on eggs, and this could be a problem for the concentrated-changes tests. However, it is unclear how additions of species to the egg-eating category would affect the results. Resolution of this issue will have to await more data.

We used a single estimate of snake phylogeny, which may seem unwise, given current disagreements about relationships among major snake lineages (e.g., Lee and Scanlon 2002; Vidal and Hedges 2002b). However, the use of alternative higher-level relationships should have only slight effects on the results, because placements of major branches have little influence on the number of origins of egg eating and on the number of branches characterized by feeding on the corresponding animals. To verify this

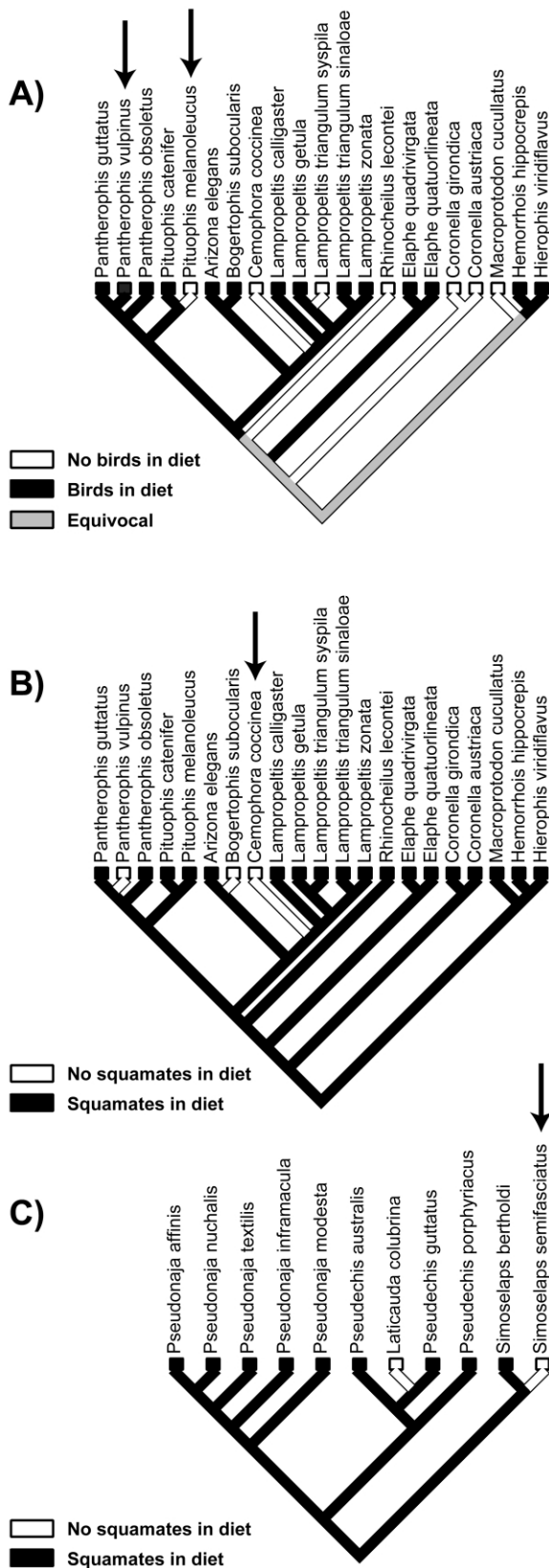
we repeated the all-taxa analyses, using the relationships from Vidal and Hedges (2002b) rather than those from Lee and Scanlon (2002) that we had initially used. The concentrated-changes results (not shown) were virtually identical to those reported above. Ambiguities closer to the tips of the phylogeny could have more substantial effects, but, as noted above, we resolved such ambiguities in a conservative manner.

Mechanisms

The results described above suggest that a snake species is more likely to become an egg eater if its diet already includes the animals that lay the eggs. Here we elaborate on the two possible, not mutually exclusive, explanations for this pattern that we raised in the introduction to this article: correlated occurrence and a specific feeding predisposition.

The notion of correlated occurrence is that a novel food type is more likely to be encountered, and thus more likely to be eaten, if its density is correlated with the density of some typical food of the organisms in question. Because of the direct connection between eggs and the corresponding animals, correlations between the densities of these potential food types presumably occur among large geographic regions and also among habitats within such regions. Correlations at the regional level may have some role in generating the observed associations between feeding on eggs and feeding on the corresponding animals. For example, perhaps many Australian elapids eat both squamates and squamate eggs because these snakes happen to occur in a region where squamates are relatively abundant (Shine 1977, 1991a). However, the facts that supporting data points for both the bird-first and squamate-first predictions are spread over several continents (Asia, Australia, and North America for birds; these three plus South America for squamates) and that they include both temperate and tropical origins argue against regional effects as a comprehensive explanation.

Correlated occurrence caused by differences among habitats within regions may be a more likely explanation for the observed feeding associations. Particular snake taxa typically are restricted to certain habitats, and this restriction undoubtedly affects encounter rates with potential prey. Aquatic snakes provide a possible example. The fact that aquatic snakes rarely eat squamates, birds, or their eggs, regardless of the general region in which these snakes occur, may be due to low densities of these prey (except for birds that are too large for most snakes to eat) in aquatic habitats. The absence of feeding on eggs and on the corresponding animals by aquatic snakes contributes to the overall positive associations observed between feeding on these two types of food.



The fact that the observed feeding associations remain when the analyses are restricted to snakes that are likely to encounter eggs and are large enough to eat them suggests that, in addition to correlated occurrence, specific feeding predispositions may be involved. One obvious possibility is that searching for squamates or birds sometimes leads snakes to the associated eggs. Like the explanations based on correlated occurrence, this searching hypothesis requires a spatial association between eggs and the corresponding animals. However, unlike those explanations, this hypothesis focuses on a specific feeding trait, namely, searching specifically for squamates or birds. The hypothesis seems especially plausible for birds because of their extended physical association with their eggs. Although egg attendance by adults is rare in squamates (Shine 1988), snakes might be led to unhatched squamate eggs by cues from hatchlings in the same clutch.

Here we develop more fully another hypothesis involving a specific feeding predisposition. In general form, the hypothesis is that, for animals that use chemical cues to recognize food, incorporation of a novel food type into the diet is more likely if the novel food produces one or more chemicals used as cues to recognize typical food. Snakes have well-developed chemosensory systems, and, as noted above, most species probably use chemical cues during some stage of prey recognition (Burghardt 1990; Ford and Burghardt 1993; Schwenk 1994). In some snakes, chemical cues from typical prey will elicit attacks on atypical prey or even inanimate objects. For example, some *Nerodia* (North American water snakes) and *Thamnophis* will bite cotton swabs that have been soaked in extracts made from typical prey of these snakes (Burghardt 1990). Furthermore, quantitative genetic studies have shown both phenotypic and genetic correlations between chemoreceptive responses to different kinds of prey by *Thamnophis elegans* (Western terrestrial garter snake; Arnold 1981). These observations raise the possibility that snakes in nature may begin feeding on novel prey because of a chemical resemblance of the novel food to typical prey (Arnold 1981; Cadle and Greene 1993).

A natural example of a chemically mediated feeding change has been suggested for *Thamnophis sirtalis* (com-

Figure 1: Origins of bird-egg and squamate-egg specialist snake species (arrows) in relation to the habit of feeding on the corresponding animals. Only the relevant parts of the snake supertree are shown, but the character reconstructions are from analyses using the entire supertree. A, Origins of the bird-egg specialist colubrine snakes *Pantherophis vulpinus* and *Pituophis melanoleucus* in relation to the habit of feeding on birds. B, Origin of the squamate-egg specialist colubrine snake *Cemophora coccinea* in relation to the habit of feeding on squamates. C, Origin of the squamate-egg specialist elapid snake *Simoselaps semifasciatus* in relation to the habit of feeding on squamates.

mon garter snakes) on certain islands in Lake Michigan (Greenwell et al. 1984). On the mainland, common garter snakes rarely eat birds, but island snakes feed heavily on nestling *Sterna hirundo* (common terns). Island snakes do not react strongly to chemical cues from birds and generally do not attack birds presented to them in captivity. However, tern nestlings are likely to be tainted with the scent of the fishes that adults feed to the young; the garter snakes presumably recognize the nestlings as prey because of the associated scent of fishes, which are more typical prey of garter snakes.

These observations suggest that, if eggs and the animals that lay them produce some similar chemical cues, then snakes that feed on the animals may also recognize the eggs as suitable food. The chemical similarity could be inherent in the eggs and animals, or it could arise from contact of the adults with the eggs. This hypothesis is attractive because it explains not only the observed associations between feeding on eggs and feeding on the corresponding animals but also why eggs, whose form and immobility strongly distinguish them from most prey of snakes, are eaten by snakes at all. A plausible variant of this hypothesis is that snakes eat eggs because of an attraction to the scent of adult prey emanating from the area around the eggs (whether a nest or otherwise) rather than from the eggs themselves.

To our knowledge, the island garter snake case is the only reported vertebrate example of a natural, beneficial feeding transition initiated through the chemical resemblance of novel prey to typical prey. However, the phenomenon has been well studied in phytophagous insects, in which the most striking examples involve host shifts between distantly related and morphologically dissimilar plants that share distinctive secondary compounds (Ehrlich and Raven 1964; Berenbaum 1983; Futuyma and McCafferty 1990; Becerra 1997; Wahlberg 2001). Studies of the cues used by insects to recognize host plants (Thorsteinson 1960; Bernays and Chapman 1994) suggest that parallel work involving egg-eating snakes would be informative. In particular, future research could include experiments to determine whether snakes use the same chemical cues to recognize eggs and the corresponding animals as food.

It is worth emphasizing that the above mechanisms directly concern the initiation of egg eating, not subsequent evolutionary adaptation and specialization. In fact, the mechanisms just described do not require any evolutionary change within populations that already feed on the relevant animals. However, these mechanisms, by promoting the initiation of egg eating, could set the stage for selection to shift feeding preferences toward eggs and to produce traits that facilitate ingestion and further processing of eggs. In other words, these mechanisms could be the cat-

alysts for the evolution of taxa such as the bird-egg specialists of the genus *Dasypeltis* and the squamate-egg specialists of the *Simoselaps semifasciatus* group, with their impressive adaptations for egg eating (Gans 1952; Scanlon and Shine 1988).

Eating Bird Eggs versus Eating Squamate Eggs

The striking morphological adaptations of African egg-eating snakes (*Dasypeltis*) have focused much attention on the habit of eating bird eggs (e.g., FitzSimons 1962; Carr 1963; Gans 1974; Greene 1997). However, for snakes in general, feeding on bird eggs is much less common than feeding on squamate eggs; for example, in our data set, 45 species ate squamate eggs, whereas only 16 ate bird eggs.

The scarcity of snakes that feed on bird eggs may be explained in part by the difficulties of swallowing these hard and often relatively large objects whole. Squamate eggs do not present such a challenge for two reasons. First, they tend to be smaller than bird eggs and are pliable (except those of most geckos) and thus can be swallowed whole more easily than bird eggs. Second, some snakes can slit open pliable squamate eggs and then either ingest their contents without the shells or collapse the slit eggs and more easily ingest them with the shells; several snake species that frequently eat squamate eggs have evolved bladelike teeth that are used for these purposes (McDowell 1972; Broadley 1979; Scanlon and Shine 1988; Coleman et al. 1993). This difference in ease of ingestion is reflected in our logistic regression results (not shown): snake body size is positively related to eating bird eggs but not to eating squamate eggs. In short, many snakes that can eat squamate eggs probably are too small to eat bird eggs.

Our results also suggest a less obvious reason why feeding on bird eggs is much less common than feeding on squamate eggs. If the habit of egg eating typically arises from the habit of eating the corresponding animals, then the number of origins of egg eating (and, indirectly, the number of egg-eating species) should reflect the number of species that eat the corresponding animals. Our data fit this expectation. Using either all taxa or excluding aquatic species and species smaller than the smallest species that ate birds, both the number of origins of feeding on bird eggs and the number of species that eat birds are substantially less than the number of origins of feeding on squamate eggs and the number of species that eat squamates (fig. 2). The results using the reduced data set are especially significant because they suggest that, even among species that are large enough to eat birds, many more species eat squamates than eat birds. This difference might reflect the earlier evolutionary origins of feeding on squamates (Greene 1983), coupled with phylogenetic niche conservatism (Harvey and Pagel 1991) and/or the diffi-

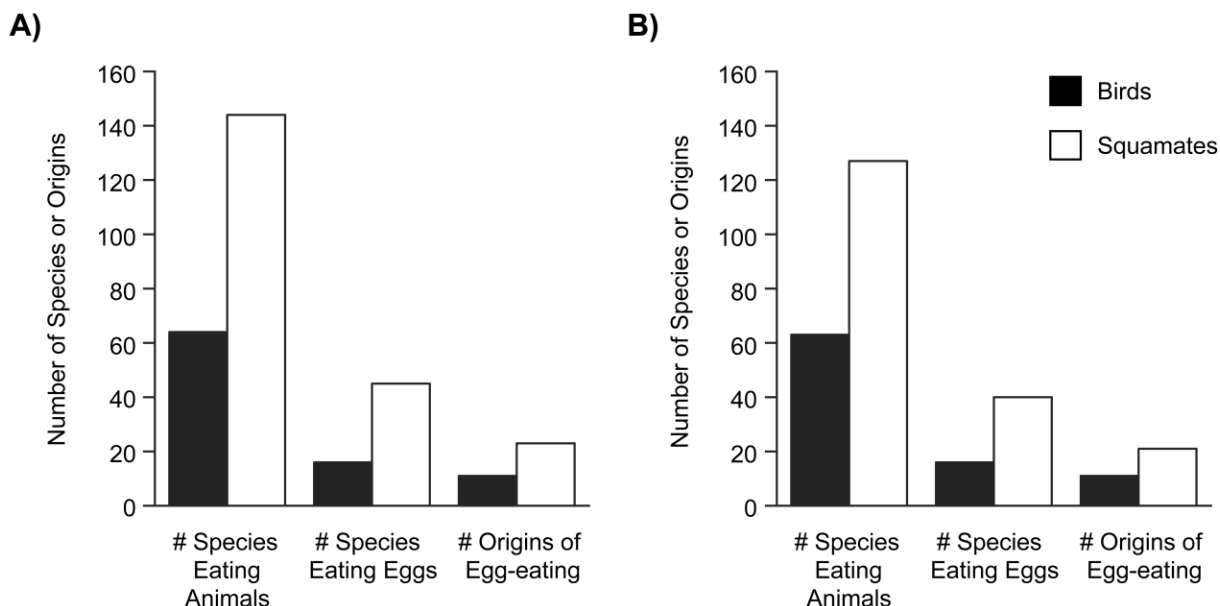


Figure 2: Numbers of snake species that ate birds, squamates, and the corresponding eggs and numbers of origins of bird egg eating and squamate egg eating. The numbers of origins are means of the DELTRAN and ACCTAN (“delayed transformation” and “accelerated transformation,” respectively) character reconstructions. *A*, Using the 198 species for which presence/absence of bird eggs in the diet was unambiguous. *B*, Using the 147 terrestrial and arboreal species with a maximum total length at least as great as that of the smallest species that ate birds.

culties of capturing, subduing, and ingesting birds (Cundall and Greene 2000). In any case, we suggest that the relative paucity of bird-eating snakes limits opportunities for the initiation of feeding on bird eggs.

The relatively small pool of snake species that eat bird eggs at any frequency might, in turn, help explain why the habit of feeding exclusively or almost exclusively on bird eggs has evolved so rarely. Such extreme specialization for feeding on bird eggs has evolved only once or twice (depending on whether *Dasypeltis* and *Elachistodon westermanni* [Indian egg-eating snake] represent the same origin of egg eating or not), compared to at least seven likely origins of extreme specialization for feeding on squamate eggs (in some *Oligodon*, *Phyllorhynchus*, some *Stegonotus*, *Enulius* [long-tailed snakes; Scott 1983 and N. J. Scott, personal communication], *Umbrivaga* [tropical forest snakes; Roze 1964], *Prosymna*, and the *Simoselaps semifasciatus* group). Previous hypotheses for the scarcity of bird-egg specialists have focused on the peculiar ecological requirements of these taxa, such as year-round availability of eggs (Pitman 1938) or the occurrence of large colonies of weaver birds (Greene 1997). Our explanation instead emphasizes that the origin of bird-egg specialists may be constrained by the nature of the evolutionary pathway to such specialization.

Importance of Historically Contingent Predispositions

Exploitation of a resource must be related in some measure to the distribution of the resource; for example, egg eating at any frequency obviously requires the availability of eggs, and obligate egg eating requires enough eggs to sustain a population of such specialists. However, the likelihood that an available resource will be exploited also may depend on organismal predispositions. We have suggested that feeding on squamates or birds predisposes a snake lineage to feed on the eggs of these animals, perhaps because of chemical similarities between the eggs and the corresponding animals. In short, origins of egg eating and, by extrapolation, of obligate egg eating may depend not only on the availability of eggs but also on the commonness of snakes that are predisposed to feed on eggs.

Cadle and Greene (1993) pointed out that differences among taxa in the tendency to exhibit a particular feeding habit can have important consequences for community composition. For example, they suggested that the lack of arthropod-eating snakes in many Neotropical communities results from the absence of snake clades with tendencies to feed on arthropods rather than from the paucity of suitable arthropods. Predispositions for or against egg eating could have similar consequences. For instance, feeding on birds seems to be especially common in certain

snake groups, such as colubrids and pythonines; thus, the frequency of bird-egg-eating species in a particular area could depend on the frequency of members of these taxa.

We have argued above that habitat use and specific feeding traits likely are important influences on the origins of egg eating. Both of these characteristics can be viewed as predispositions that are the results of a lineage's specific evolutionary history. For example, arboreality and an attraction to chemical cues produced by birds are not simply properties of any snake that finds itself in a forest with many birds but are outcomes of a contingent evolutionary pathway. Thus, the effects of such predispositions are part of the general imprint of history (Cadle and Greene 1993; Farrell and Mitter 1993). Other studies also have emphasized the influence of history on the ecological characteristics of communities and larger biotas (Shine 1983; Henderson and Crother 1989; Cadle and Greene 1993; Farrell and Mitter 1993; Rodríguez-Robles and Greene 1996; Price et al. 2000; Webb et al. 2002; Vitt et al. 2003; Vitt and Pianka 2005). Our particular contribution is in documenting patterns indicating specific historically contingent biases in the pathway to a novel feeding habit.

Acknowledgments

We thank M. Packard for identifying eggs from *Thamnophis* stomachs; N. Scott for diet records of *Enulius*; D. Creer, J. Fetzner, and R. Lawson for access to unpublished phylogenetic studies; O. Sexton for pointing out a key reference; H. Smith for access to his large herpetological library; K. Ashton, S. Boback, and R. Henderson for snake body length data; A. Meade and M. Pagel for providing their RJ-Discrete program and advice on how to use it; and two anonymous reviewers for many helpful comments on the manuscript.

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