Competition, predation and nest niche shifts among tropical cavity nesters: phylogeny and natural history evolution of parrots (Psittaciformes) and trogons (Trogoniformes)

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Nest site selection by birds is a critically important life history trait as competition for suitable sites can be intense, and because birds are at their most vulnerable to predators during nesting. Previous studies show that the clutch size and nestling period evolve in response to competition for nest sites and nest predation, respectively. This provides the opportunity to study the relative contribution of competition and predation to the evolution of nesting niche. Using previously published phylogenies for parrots and trogons, I found evidence for at least 13 independent evolutionary transitions from tree cavities to alternative nesting niches (including termitaria, cliffs, and burrows). I analyzed variations in clutch size, incubation period and nestling period for 16 phylogenetically controlled pairs of species to test the relative roles of competition for tree cavities and nest predation, in favoring evolutionary switches to alternative nest sites. Tree cavity nesting species did not have larger clutch sizes as predicted if competition for tree cavities leads birds to invest heavily in nesting once they obtain a nest site (the limited breeding opportunities hypothesis). Instead I found that shifts to alternative nesting niches were accompanied by an increase in nestling period. As nestling period is a surrogate measure for long-term nest predation rates, this finding suggests that nest predation has been more important than competition in niche diversification among cavity nesting parrots and trogons. The timing of events in South America suggests that the explosive radiation of mammalian nest predators during the Upper-Oligocene, Lower-Miocene (20–30 million years ago) corresponded with the radiation of parrot and trogon taxa that exploit novel nesting niches.

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Competition for nest sites and nest predation exert great influence on avian natural history traits including nest site selection, clutch size, and nestling period (Van Balen et al. 1982, Duffy 1983, Oniki 1985, Martin 1995, Yanes and Suárez 1997). These forces may even play causative roles in determining which species can coexist in avian communities (Martin 1988a, b, Newton 1994). Despite the importance of competition for nest sites and nest predation, their relative roles in the evolution of avian nest site selection and nest niche shifts has not been quantified. Ecological studies have shown that both competition and predation strongly influence nest selection among cavity nesting birds, making these taxa ideal for studies of the relative contribution of competition and predation to evolutionary shifts in nesting niche (Van Balen et al. 1982, Nilsson 1984).

Population dynamics and life history evolution of cavity nesting birds are supposedly dominated by competition for cavities (Martin 1993, Beissinger 1996, but see Nilsson 1984, 1986). For many secondary cavity nesting species (those that cannot excavate their own cavities), there is intense competition for nest sites (review in Newton 1994, but see Brawn and Balda 1988, Waters et al. 1990, Carlson et al. 1998). It has

been suggested that species facing constant, intense competition for nest cavities evolve larger clutch sizes (the limited breeding opportunities hypothesis; Beissinger and Waltman 1991, Martin 1993, Beissinger 1996). This is presumably because selection favors heavy investment in reproduction when the chance for future breeding opportunities is limited. Species that excavate their own nest sites are generally thought to face reduced competition for nest sites (Mönkkönen and Orell 1997, Brightsmith 2000, Collar 2001). Based on this evidence, species derived from secondary cavity nesting taxa that can exploit alterative substrates and escape from this nest site limitation should have smaller clutch sizes than those that are dependant on previously existing tree cavities.

Birds are very vulnerable to predation while in the egg or chick stage. As a result, high rates of nest predation favor rapid development and short nestling periods (Lack 1968, Bosque and Bosque 1995, Yanes and Suárez 1997). When other factors such as body size and phylogeny are controlled, differences among nestling periods apparently reflect differences in the intensity of nest predation faced over evolutionary time (Bosque and Bosque 1995, Martin 1995). Natural selection should favor evolutionary shifts into novel nesting niches where nest predation rates are lower. For this reason, comparisons of nestling periods should give an indication as to whether nest predation rates have favored nest niche diversification through the exploitation of novel nesting niches.

The orders Trogoniformes (trogons and quetzals) and Psittaciformes (parrots, lories, cockatoos, etc.) are composed almost exclusively of cavity nesting birds (Skutch 1981, Collar 1997, Juniper and Parr 1998). While many members of these families use previously existing cavities, some members of both orders have evolved the ability to excavate in a variety of different substrates. Some trogons excavate cavities in soft rotting trees, termite mounds, or the nests of other social insects (Brightsmith 2000, Collar 2001) while some parrots use cliffs, ground burrows or termite mounds (Arndt 1992–1996, Collar 1997, Juniper and Parr 1998). This diversity in nesting substrates coupled with published phylogenies makes these families ideal to study the evolution of nest site selection (Espinosa de los Monteros 1998, Russello and Amato 2003, Ribas and Miyaki 2004).

I use phylogenetically controlled analyses of parrots and trogons to investigate the following hypotheses: 1) tree cavity nesting is the ancestral state for parrots and trogons, 2) species that excavate nest cavities in termitaria lay smaller clutches than those dependant on previously existing tree cavities, and 3) species nesting in evolutionarily novel nesting niches have longer

nestling periods indicating that they suffer from lower rates of nest predation.

Methods

Phylogenies

I obtained previously published phylogenies for Australo-Pauan parrots (Rowden 1996, Christidis et al. 1991), African lovebirds (genus *Agapornis*, Eberhard 1989), New World parrots (Miyaki et al. 1998, Russello and Amato 2003, Ribas and Miyaki 2004), and trogons (Espinosa de los Monteros 1998). The Austalo-Papuan parrot phylogenies included a consensus tree based on 773 bp of cytochrome b and 16S rDNA sequences of 6 *Neophema* parakeet species including the burrow nesting *N. petrophila* (Rowden 1996) and a strict consensus tree using 21 protein loci including 23 species representing of which 8 use alternative nesting substrates (Christidis et al. 1991). The latter phylogeny contained many unresolved nodes, which prevented determination of the direction of evolutionary shifts in substrate use for many taxa. The African lovebird phylogeny was a maximum parsimony tree based on 622 bp of the mitochondrial cytochrome-b gene containing 8 members of the genus *Agapornis* including the termitarium nesting *A. pullarius*. I used two New World parrot phylogenies. One was a strict consensus tree based on 3,160 pb from 3 mitochondrial and 3 nuclear DNA regions including 31 species of which 25 were from the genus *Amazona* (Russello and Amato 2003). Seven taxa used alternative nesting substrates, three of which used termitaria (Fig. 1). The other New World parrot phylogeny was a strict consensus tree based on 2,029 bp of mtDNA from 4 regions (Ribas and Miyaki 2004). The tree included 16 species of the long-tailed parrot clade including 6 from the genus *Aratinga* of which 3 species used termitaria and 2 used cliff burrows (Fig. 2). An additional New World parrot phylogeny was reviewed but it did not contain novel information (Miyaki et al. 1998).

The trogon phylogeny is based on the single most parsimonious tree from 1,778 bp of mitochondrial cytochrome B and 12S rRNA genes (Espinosa de los Monteros 1998). It includes members of all 6 of the extant trogon genera, and 20 of the 39 species (Fig. 3). Nesting behaviors show little variation within genera except for *Trogon* so each genus was collapsed and presented as a single taxon (except *Trogon*). Of the seven species of the genus *Trogon* that are not in the original phylogeny, three were inserted based on their similarities to included taxa. *T. bairdii*, and *T. aurantiiventris* have been considered subspecies or sibling
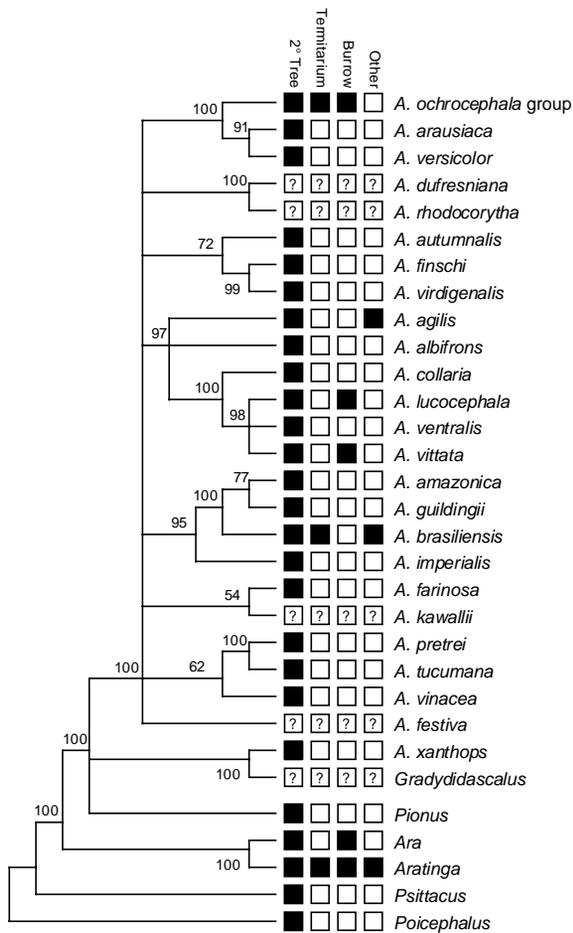
Fig. 1. Partial phylogeny of nesting behavior of *Amazona* and related parrots. The phylogeny is the strict consensus of 12 equally parsimonious trees based on 3,160 bp from 3 mitochondrial and 3 nuclear DNA regions from Russello and Amato (2003). The numbers at the nodes represent the bootstrap values from the original analysis. Data are presented on the nest substrates used: previously existing tree cavities (2° Tree), termitaria, burrows in cliffs or the ground, and other substrates (including the bases of epiphytes, and bases of palm fronds on palm trees). "?" indicates that the nesting behavior for the species is unknown. The "A. ochrocephala group" consists of 5 different "species" that were found to be polyphyletic in the original analysis (Russello and Amato 2003).
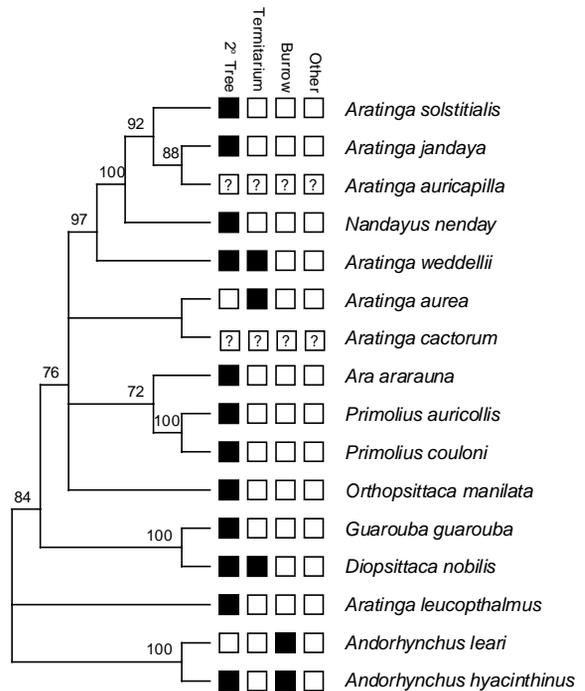

Fig. 2. Partial phylogeny of the nesting behavior of the long-tailed clade of New World parrots. The phylogeny is a maximum parsimony, strict consensus tree based on 2,029 bp from 4 regions of mitochondrial DNA (Ribas and Miyaki 2004). The numbers represent the bootstrap values from the original analysis. Data are presented on the nest substrates used: previously existing tree cavities (2° Tree), termitaria, burrows in cliffs or the ground, and other substrates (including the bases of epiphytes, and bases of palm fronds on palm trees). "?" indicates that the nesting behavior for the species is unknown.

species of *T. viridis* and *T. collaris* respectively, differing only in the color of the belly (Skutch 1962, Sibley and Ahlquist 1990). Similarly *T. massena* is thought to be conspecific with taxa currently included within both *T. melanurus* and *T. comptus* (Sibley and Monroe 1990). The close relationship of these taxa is also supported by phylogenetically informative plumage characteristics (Sibley and Monroe 1990, Espinosa de los Monteros 1998).

For each phylogeny I collapsed all nodes that had bootstrap support of less than 50% and mapped the occurrence of secondary tree cavity nesting (using old

tree cavities), primary tree cavity nesting (excavating new cavities), burrow nesting and cliff nesting (lumped under the heading "burrow"), termitarium nesting, and all other types of novel nesting behaviors (lumped under the heading "other"). Ancestral states were reconstructed using simple parsimony analyses to determine the directions of transitions in nesting behavior.

Nesting data

I compiled parrot nesting data from recent reviews (Arndt 1992–1996, Collar 1997, Juniper and Parr 1998). Taxa were recorded as using a substrate if I could locate any record of its use without regard to the frequency with which it was used. In most instances I could not score species on the frequency with which they use substrates because of the general paucity of nest records for parrots. Most species that nest in termitaria excavate their own cavities although use of old cavities in termitaria by secondary cavity nesters has been recorded (Hindwood 1959, Collias and Collias 1984, Collar
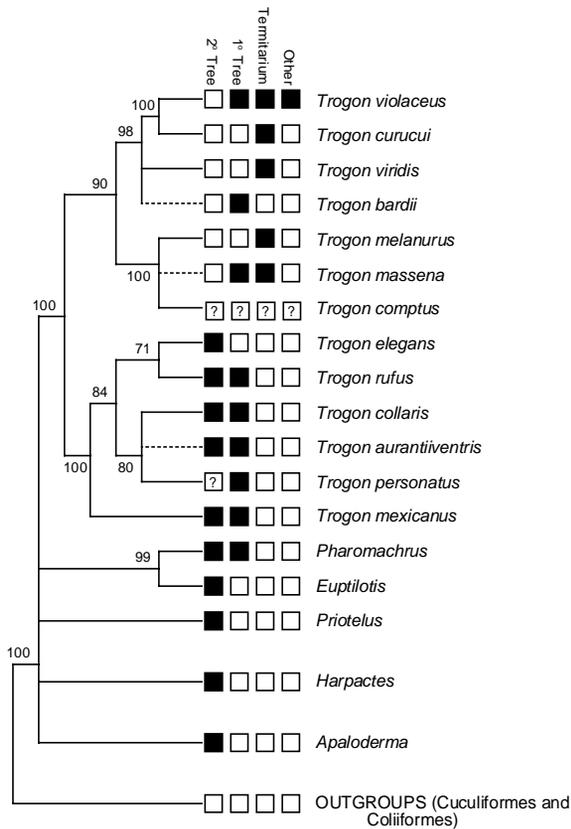
Fig. 3. Phylogeny of trogon nesting niches. The phylogeny is based on the single most parsimonious tree produced from 2,1591 bp of cytochrome b and 12S rDNA (Espinosa de los Monteros 1998). The numbers represent the bootstrap values from the original analysis. Taxa marked with dotted lines were not included in the original analysis but are included because all have been considered subspecies or sibling species of included taxa (see text). Data are presented on use of old tree cavities (2° Tree), cavities excavated by the breeding pair (1° Tree), arboreal termitaria and nests of social insects other than termites (other social insects). Black squares indicate that members of the taxon regularly use the nesting substrate, white squares indicate the taxon does not use the substrate, and the hatched squares indicate that the behavior has been recorded only for populations living on Trinidad (ffrench 1991). The nest site for *T. comptus* is unknown. For *T. personatus*, it is known to use tree cavities but not whether it excavates cavities or uses old ones. *T. mexicanus* excavates new cavities, but it is uncertain if it uses old cavities as well.

1997). As a result, I assume throughout that all parrots recorded as using termitaria for nesting are capable of excavating their own holes in this substrate unless explicitly stated otherwise in the source.

Nesting data for trogons were compiled from the detailed accounts of Skutch and supplemented by regional bird guides and monographs (Skutch 1942, 1948, 1959, 1972, 1981, 1983, 1999, Haverschmidt 1968, Wetmore 1968, Hilty and Brown 1986, Styles and Skutch 1989, Howell and Webb 1995, Collar 2001). Trogons were scored as secondary cavity nesters if they used old

tree cavities, primary tree cavity nesters if they excavated their own nests in trees, and termitarium nesters if they excavate their own cavities in termitaria. Species could be classified under more than one of these three divisions. As with parrots, scarcity of nesting records prevented scoring species based on their relative use of different substrates.

I tested whether species that use novel nesting substrates have longer nestling periods. I used data on 16 parrot genera, which contain species that nest in tree cavities (the ancestral characteristic) and a novel nesting substrate (Appendix 2, termitaria N = 7, burrows N = 5, cliffs N = 3, and between palm leaves N = 1). One additional contrast was used: *Diopsittaca nobilis* (red-shouldered macaw) which occasionally uses termitaria was contrasted with the slightly larger *Guarouba guarouba* (golden parakeet) as these are apparently sister taxa (Fig. 2, Ribas and Miyaki 2004).

Data analysis

Detailed phylogenies of individual genera were not available to allow precise phylogenetic control of most pairs, so to be conservative, I generated only one independent contrast per genus. For each contrast I compared the nestling period of one species that uses a novel nesting substrate to a congener of the same size or slightly larger that uses only tree cavities. I used larger species when possible to be conservative because larger body size correlates with longer nestling period independent of the effects of predation (Martin 1995). If there was no species the same size or less than 20% larger, I used the species that was closest in size. This generated some pairs for which the species that uses novel nesting substrates were larger and some pairs where the size differences exceeded 20%. If there were multiple species in the genus that used the novel nesting substrate each was paired with a tree cavity nester and the pair that differed the least in size was used in the analysis. For the genus *Agapornis* a detailed phylogeny was available and the termitarium nester *A. pullaria* was paired with the species closest in size *A. lilianae* not its sister species *A. taranta* which is over 40% heavier (Eberhard 1998). I paired species based on mass, when available (Dunnings 1992, Collar 1997). For species lacking mass data, total body length was used to pair similarly sized congeners. When available, nestling periods from wild nests were used (N = 7 species), but in most instances such data were lacking, so the data from captive pairs presented in Arndt (1992–1996) or Collar (1997), were used.

The analyses were repeated using incubation period because high predation rates selecting for shortened nestling period could also act to shorten the incubation period (Bosque and Bosque 1995). This analysis was also repeated using clutch size. This was done to test the prediction that species able to excavate their own nest cavities have smaller clutch sizes than those that rely on existing tree cavities, as predicted by the limited breeding opportunities hypothesis (Beissinger and Waltman 1991, Martin 1993, but see Mönkkönen and Orell 1997).

For three genera there were two or more equally acceptable pairs with similar or identical body sizes. In all three of these cases, the different pairs gave different results for one or more of the variables of interest (clutch size, nestling period, or incubation period). When the pairs gave conflicting results, the P-value was calculated scoring the comparison in each possible combination. The resulting P-values were then averaged.

Results

Phylogenies

Phylogenetic analyses suggest that at least 13 independent evolutionary transitions from nesting in tree cavities to nesting in alternative nesting substrates and 8 independent transitions to nesting in termite mounds. The basal taxa in the phylogenies are secondary cavity nesters suggesting this as the ancestral state for all lineages. The phylogenies for Australo-Papuan parrots suggest that burrow nesting *Neophema petrophila* (Rowden 1996) and termitarium nesting *Psephotus* arose from tree cavity nesting ancestors (Christidis et al. 1991). Similarly the termitarium nesting *Agapornis pullarius* is descendent from tree cavity nesting congeners (Eberhard 1998).

The phylogeny of the genus *Amazona* suggests that the use of alternative nesting substrates arose four times in the genus: termitarium and burrow use in the *A. ochrocephala* group, termitarium and epiphyte use in *A. brasiliensis*, epiphyte use in *A. agilis*, and burrow use in *A. lucocephala* and *A. vittata* (Fig. 1). The phylogeny of the long-tailed clade of New World parrots suggests at least 3 independent origins for use of alternative nesting substrates: cliff nesting in *Andorhynchus*, termitarium nesting in *Diopsittaca* and termitarium nesting in *Aratinga* (Fig. 2).

The phylogeny of trogons suggests that secondary cavity nesting was the ancestral character state and that the common ancestor of *Pharomachrus*, *Euptilotis* and *Trogon* was a primary cavity nester (Fig. 3, ffrench 1991,

Zimmerman et al. 1996, Espinosa de los Monteros 1998, Grimmett et al. 1999). The members of the genus *Trogon* are divided into two monophyletic subclades: the "Elegant subclade" composed of species that use old cavities or excavate new ones, and the "Violaceus subclade" with predominantly termitarium nesting species (Wetmore 1968, Skutch 1972, 1981, 1999, Styles and Skutch 1989). This phylogeny suggests two independent origins of termitarium nesting (ancestor of the Violaceous subclade and *T. collaris*), four independent losses of primary cavity nesting (*Euptilotis neoxenus, T. elegans, T. melanurus*, and the *T. violaceous/T. curucui* common ancestor), and one loss of termitarium nesting (*T. bardii*).

Natural history traits

Parrot species that use alternative nesting substrates like cliffs, burrows or termitaria have longer nestling periods than those that use old tree cavities (sign test: novel longer =11.5, tree longer =0, tie =4.5, P <0.001, Table 1). When only termitaria/tree cavity pairs are considered, termitarium nesters have significantly longer nestling periods (sign test: Table 2, termitarium longer =6.5, tree longer =0, tied =0.5, P =0.02).

The members of the genus *Trogon* were not included in the above analysis, but show a trend similar to the parrots. The 90 g *T. melanocephalus* nests in termite mounds and fledges in 16 to 17 days (Skutch 1983, Styles and Skutch 1989). The 56 g *T. violaceous* nests in wasp nests, ant nests, termitaria and other sites and fledges in 17 days or more (Styles and Skutch 1989, Skutch 1999). These periods are slightly longer than the tree cavity nesting 69 g *T. mexicanus* (15 days) and 57 g *T. rufous* (14 days; Skutch 1983).

Parrot species that use tree cavities and alternative nesting substrates did not differ in clutch size (sign test: novel larger =5.8, tree larger =6.7, tie =3.5, P =1.0, Table 1), nor incubation period (sign test:

Table 1. Life history traits of parrots nesting in tree cavities and novel nesting substrates. Differences in nestling period, clutch size and incubation period are presented for congeners that nest in only tree cavities versus those that can nest in novel substrates. Species were paired for size. Differences were tested using the sign test procedure (Gibbons 1985). See text for details on how the pairs were scored and P-values calculated. Raw data for these analyses are reported in the Appendix.

| | Novel nester | | Tie | P |
	Greater	Less		
Nestling period	11.5	0	4.5	0.0008
Clutch size	5.8	6.7	3.5	0.89
Incubation period	5	5	5	1.0
Body size	8.3	4.7	3	0.47

Table 2. Life history traits of parrots nesting in tree cavities and termitaria. Difference in nestling period, clutch size and incubation period for congeners that nest in only tree cavities vs those that can nest in termitaria. Species were paired for size. Differences were tested using the sign test procedure (Gibbons 1985). See text for details on how the pairs were scored and P-values calculated. Raw data for these analyses are reported in the Appendix.

| | Term. nester | | Tie | P |
	Greater	Less		
Nestling period	6.5	0	0.5	0.02
Clutch size	3.8	1.7	1.5	0.67
Incubation period	2	2	3	1.0
Body size	2.7	2.3	2	1.0

novel longer = 5, tree longer = 5, tie = 5, P = 1.0). The results were similar when the analysis was confined to just comparisons between termitarium and tree cavity nesting parrots (sign test: clutch size termitarium larger = 3.8, tree larger = 1.7, tie = 1.5, P = 0.67; incubation period termitarium longer = 2, tree longer = 2, tie = 3, P = 1.0, Table 2).

Discussion

Phylogenetic analyses suggest that tree cavity nesting is the ancestral state among parrots and trogons and that most genera have independently evolved the ability to exploit novel nesting substrates. Most of the taxa capable of using alternative nesting substrates also retain the ability to nest in tree cavities (75%, N = 16), showing that the species have actually evolved a phenotypic plasticity that allows them to exploit multiple nesting substrates. There are few published nesting records for most parrot species, so the possibility remains that other species will be found nesting in alternative nesting substrates. These future nesting records and forthcoming phylogenies should be used to test the finding of this paper that use of alternative nesting substrates is independently evolved in most genera.

The limited breeding opportunities hypothesis

I hypothesized that if competition for tree cavities was driving birds to use alternative nesting substrates I would find higher clutch sizes among species using termitaria and other alternative nesting substrates. However, contrary to the predictions of the limited breeding opportunities hypothesis, this was not the case. The limited breeding opportunities hypothesis postulates that species facing high competition for nest sites should invest more in each nesting attempt (i.e. lay a larger clutch) when they obtain a nest site as future

breeding opportunities are not guaranteed (Beissinger and Waltman 1991, Martin 1993, Beissinger 1996, Mönkkönen and Martin 2000). The applicability of this theory to tropical taxa has not been explored. Variation in clutch size among tropical birds is greatly reduced compared to temperate species, which could limit the usefulness of clutch size analyses for tropical species (Robinson et al. 2000). However, lack of variation did not greatly affect the current analysis as >80% (N = 16) of the genera showed variation in clutch size (Table 1, Appendix). My finding that clutch size was not greater for species using alternative nesting substrates suggests either that clutch size is not a good indicator of competition for nest sites, or that competition has not favored the shift in nesting substrates. The latter possibility would hold if cavity-nesting birds did not face strong competition for nest sites or if competition for the alternative nest sites and competition for tree cavities were equally intense. Field evidence suggests that termite mounds and burrows are not limiting parrot reproduction in at least some systems (Brightsmith 2000, Masello and Quillfeldt 2002). Regardless of whether or not alternative nesting substrates are limiting, the evidence presented here does not support the hypothesis that competition for tree cavities has encouraged a diversification of nesting niches by parrots and trogons.

Predation and nest niche shifts

Nestling periods are significantly longer for species using novel nesting niches; of the 16 parrot and one trogon genera analyzed not one went against this trend (although 4.5 of the comparisons were uninformative). Most of the data used for this analysis were from captive pairs, showing that the observed differences in nestling period are heritable and not just differences in local conditions.

The finding that species using novel nesting niches have longer nestling periods supports the hypothesis that natural selection favors shifts to novel nesting niches where predation rates are lower. This assertion is based on the assumptions that: 1) other factors like food supply, body size, phylogeny, latitude and parasitism are not causing the observed variance in nestling period, and 2) nestling period correlates with nest predation. Food availability may influence fledging times of individual broods (Lack 1968), but is unlikely to cause heritable changes among similar species that use different nest substrates. Most of the natural history data used in this analysis are from captive pairs with access to unlimited food, further reducing the potential importance of food availability in producing the

observed results. Nestling period is also known to vary with body size, phylogeny, and latitude (Lack 1968, Bosque and Bosque 1995, Martin 1995). The present analysis was designed to control for the effects of body size and phylogeny by pairing congeners of similar size. Latitude, while not included as a criterion for choosing species, likely did not have much influence on the analysis, as members of 11 of the 16 analyzed genera showed extensive latitudinal overlap (Forshaw 1989). For the remaining five comparisons, the analysis was conservative as species using the alternative nesting substrate occurred closer to the equator where nestling periods are usually shorter (Martin 1995).

The contention that nestling period is inversely related to nest predation rate was first proposed by Lack (1968). Empirical support comes from a study of 101 North American bird species (Martin 1995), comparisons of related island and mainland species (Bosque and Bosque 1995), and 31 species from the Iberian Penninsula (Yanes and Suárez 1997). In all three studies species with greater average nest predation rates showed shorter nestling periods. A review of wild parrot nesting shows that the Burrowing Parrot has a nestling period 11 days longer than predicted based on body size, nests in burrows in limestone cliffs and has the lowest predation rate yet documented among psittacines (Masello and Quillfeldt 2002). These studies suggest there is a causal link between nest predation and nestling period across many taxa and a broad range of ecological conditions.

Additional evidence to support the hypothesis that birds nesting in alternative nest substrates suffer lower predation rates comes from a study of nest predation rates of lowland forest birds in Peru. Here natural and artificial nests in termitaria experienced much lower predation rates than those in old tree cavities (Brightsmith 1999, 2005). These field data combined with the evolutionary analyses conducted here suggest an important role for predation in molding nest site selection among trogons and parrots.

Timing of nest niche shifts

The radiation of the long-tailed clade of New World parrots is estimated to have occurred during the late Oligocene-early Miocene (20–30 million years ago (MYA), Miyaki et al. 1998). This clade radiated producing 18 genera of which 12 have members that use alternative nesting substrates (Sick 1993, Miyaki et al. 1998). This suggests that 46% (N = 26) of the parrot genera that exploit alternative nesting substrates arose during this single radiation event. Termitarium nesting among trogons may have also arisen at this time, as

the major split within the genus *Trogon* and the concomitant origin of termitarium nesting in the Violaceus subclade is thought to have occurred between 14.5 and 26 MYA (Espinosa de los Monteros pers. comm.). Amber from the Dominican Republic and Mexico show that two genera of mound building termites exploited by birds, *Constricotermes* and *Nasutitermes*, were present in the Neotropics during the Upper Oligocene-Lower Miocene (20–30 MYA) at the time of the proposed radiation of parrot and trogon taxa (Hindwood 1959, Hardy 1963, Krishna and Weesner 1970, Brightsmith 2000, 2004).

The period from 20–30 MYA also saw great change in South American mammal communities including the appearance and rapid radiation of the New World primates, the appearance of rodents and the radiation of a number of caviomorph families including Echimyidae (tree rats), and the radiation of the arboreal, omnivorous marsupial family Caenolestidae (Carrol 1988, Pascual and Ortiz 1990, Poirier et al. 1994, Flynn et al. 1995). These three mammal groups are all important nest predators in tropical zones suggesting that the nest predator community of South America underwent major diversification 20–30 MYA (Arango and Kattan 1997, Robinson 1997, Roper and Goldstein 1997, Terborgh et al. 1997).

The great diversification of arboreal mammalian nest predators and the radiation of parrot and trogon taxa capable of nesting in alternative nesting substrates are all thought to have occurred during the same 10 million year period. Obviously 10 million years is sufficient time for multiple independent evolutionary changes to have occurred, so there need not be a causal link among these phenomena. In addition these three evolutionary events could have been independent responses to geologic or climatic changes (Miyaki et al. 1998). However the findings presented here show it is conceivable that evolutionary shifts from nesting in old tree cavities to nesting in termitaria and other novel nesting niches may have been causally related to the radiation of arboreal mammalian nest predators.

The analyses presented here included species from four continents showing that nest predation may act worldwide favoring nest site diversification among traditionally tree cavity nesting taxa. The fact that this analysis suggested a prominent role for predation and not competition was unexpected as most analyses and discussions of cavity nesting demonstrate, or imply, that competition is the dominant ecological factor molding the natural history of cavity nesting birds (Martin 1993, Newton 1994, Beissinger 1996).

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Appendix. Clutch size, incubation period, and nestling period for parrots that nest in novel nesting substrates and congeners that nest only in tree cavities. Congeners included in this table were paired based on mass when available (from Dunnings 1992). When mass was not available total length was used. All tree cavity nesters reported here use old tree cavities. Pluses, minuses and zeros in the rows next to the genus name show for each variable whether the species using the novel nesting substrate was greater (+), less than (−) or equal to (0) the value for the tree cavity nester. Data from Arndt (1992–1996), except where noted.

Substrate Genus species	Size Weight (g)	Size Length (cm)	Nesting substrate	Clutch size	Incubation (days)	Nestling period	Data source
Termitaria							
Psephotus	0/0			0/−	0/+	+/+	
dissimilis		26.5	termitarium	5	19	35	wild
haematonotus		26.5	tree	5	19	28	wild
pulcherrimus		28.5	termitarium	4	21	35	wild
varius		28.5	tree	5	19	28	wild
Poicephalus	−/+/+			+/−/−	−/−/−	+/+/+	
rufiventris	120		termitarium/tree	3	25	60	captive
cryptoxanthus	140		tree	2.5	26	56	captive
meyeri	117.5		tree	3.5	27	59.5	captive
ruppellii	117.5		tree	3.5	26	59	captive
Agapornis	−			+	+	+	
pullarius	37.5		termitarium	5	24.5	50	captive
lilianae	40.5		tree/old cup nest	4	21.5	35	captive
Diopsittaca	−			+	−	+	
nobilis		30	termitarium/tree	5	23	60	captive
Guarouba							
guarouba		35	tree	4	24	49	captive
Aratinga	0			−/+	+/0	+/0	
chloroptera		32	termitarium/tree	3	26	56.5	captive
holochlora		32	termitarium/tree	4	23	50	captive
leucopthalmus		32	tree	3.5	23	50	captive

Appendix. (*Continued*)

Substrate Genus species	Size Weight (g)	Length (cm)	Nesting substrate	Clutch size	Incubation (days)	Nestling period	Data source
Forpus	−			+	0	+	
crassirostris	26		termitarium/tree	5.5	21	35	captive
coelestis	26.2		tree	5	21	31.5	captive
Amazona	+			0	0	+	
ochrocephala	433		termitarium/tree	3	26	60	captive
autumnalis	399		tree	3	26	56	captive
Burrow/Cliff							
Nestor	+			−	−	+	
notabilis		48	burrow/tree	3	21	91	wild
meridionalis		46	tree	3.5	25.5	66.5	wild
Neophema	+			−	−	0	
petrophila	52		burrow	4.5	18	30	captive
chrysostoma	45		tree	5	18.5	30	captive
Platycercus	−			+	0	0	
eximius	105		walls, burrow/tree	5	19	35	Collar 1997
flaveolus	120		tree	4.5	19	35	Collar 1997
Cyanoramphus	+			−	+	0	
novaezelandiae		29	burrow/tree	6.5	20	35	captive
auriceps		23	tree	8	19	35	captive
Psittacula	0			−	−	+	
krameri		40	cliff, wall/tree	3.5	22	49	Collar 1997
himalayana		40	tree	4	24	40	Collar 1997
Ara	+			0	0	0	
militaris	1134		cliff/tree	2.5	26	84	captive
ararauna	1125		tree	2.5	26	84	captive
Rhynchopsitta	+			0	+	+	
terrisi		42.5	cliff	2.5	26	60	wild
pachyrhyncha		38	tree	2.5	23	55	captive
Bolborhynchus	−			+	+	+	
orbygnesius	49		burrows	5	23	45.5	captive
lineola	53.6		tree	4.5	20.5	42	captive
Other							
Psitteuteles	+				−	?	+
goeldiei		19	palm leaves	2	?	42	captive
versicolor		18	tree	3	22	38.5	captive