

CAVITY ADOPTION AND THE EVOLUTION OF COLONIALITY IN CAVITY-NESTING BIRDS

JESSICA R. EBERHARD¹

Smithsonian Tropical Research Institute, Apdo. 2072, Balboa, Republic of Panama

Abstract. Among cavity-nesting birds, a distinction can be made between excavators, which dig their own cavities, and cavity-adopters, which nest in pre-existing cavities. Historically, these two types of species have been grouped together as “cavity-nesters,” but it has become clear that the two nesting habits are associated with very different suites of life-history characters. This paper tests the hypothesis that cavity-adopters differ from excavators and other nest-building species in their propensity to evolve colonial breeding. Because of their dependence on pre-existing cavities, cavity-adopters presumably have less control than excavators over the location of their nests, and this could limit their ability to nest near conspecifics. A literature survey of the nesting behavior of 842 species in 17 bird families shows that coloniality almost never occurs in species that are obligate cavity-adopters. A phylogeny-based comparative analysis of nesting behavior in the Anseriformes indicates that in this group, colonial breeding has evolved less frequently in lineages of cavity-adopters than would be expected by chance. Together, this evidence supports the hypothesis that colonial breeding systems are unlikely to evolve in lineages of cavity-adopters.

Key words: *Anseriformes, birds, cavity nesting, colonial nesting, comparative method.*

Evolución de la Colonialidad en Aves que Nidifican en Cavidades

Resumen. Las aves que nidifican en cavidades pueden dividirse en dos grupos: las especies excavadoras, que construyen sus propias cavidades, y las no-excavadoras, que nidifican en cavidades pre-existentes. Históricamente, estos dos tipos de especies han sido agrupadas colectivamente como aves que anidan en cavidades, pero estudios recientes demuestran que los dos tipos de nidificación están asociados con diferentes caracteres de sus historias de vida. En este estudio se pone a prueba la hipótesis que especies no-excavadoras difieren de las excavadoras y de otras especies que construyen nidos en cuanto a su propensión a evolucionar hábitos de reproducción colonial. Debido a que dependen de cavidades pre-existentes, las especies no-excavadoras presumiblemente tienen menos control que las excavadoras sobre la ubicación de sus nidos, y esto podría limitar su habilidad para nidificar cerca de otros miembros de su especie. Una revisión bibliográfica sobre el comportamiento de nidificación de 842 especies pertenecientes a 17 familias demuestra que casi nunca se observa colonialidad en especies que obligatoriamente utilizan cavidades pre-existentes. Un análisis comparativo utilizando una filogenia y datos del comportamiento de nidificación de miembros del orden Anseriformes indica que la colonialidad ha evolucionado con menor frecuencia de lo esperado al azar en linajes de especies no-excavadoras que utilizan cavidades. En conjunto, estos datos apoyan la hipótesis que los sistemas de nidificación colonial tienen baja probabilidad de evolucionar en linajes de no-excavadoras que anidan en cavidades.

INTRODUCTION

The great diversity of nests used by birds includes the huge mounds of soil and decaying vegetation used by megapodes; cavities in trees or among rocks; burrows in the ground, in

banks, or in termitaria; cup and domed nests built with materials such as twigs, grass, mud, and spider silk; and elaborately woven nests like those built by weaverbirds, orioles, and oropendolas (Collias and Collias 1984). Among cavity-nesters, a distinction can be made between excavators (which dig their own cavities) and cavity-adopters (which nest in pre-existing cavities). These two types of cavity-nesters have historically been grouped together as having a single nest type, but it has become clear that the distinction is an important one to make when studying the evolution of cavity-nesting lineages.

Manuscript received 11 June 2001; accepted 11 January 2002.

¹Present address: Macaulay Library of Natural Sounds, Cornell Laboratory of Ornithology, 159 Sapsucker Woods Rd., Ithaca, NY 14850. E-mail: jre24@cornell.edu

Excavators differ from cavity-adopters in a number of life-history traits, including nesting success, clutch size, duration of incubation and nestling periods, annual productivity, and adult survival (Martin and Li 1992). In a study of life-history traits of North American Passeriformes and Piciformes, Martin (1995) found that variation in fecundity and adult survival is better explained by nest sites, and their associated nest predation, than by food limitation. In fact, when adult survivorship and annual fecundity are compared among species representing an array of nest types, excavators rank among the highest in survivorship and lowest in fecundity, while cavity-adopters generally have low survivorship and high fecundity (Martin 1995). In the case of cavity-adopters, larger clutch sizes may have resulted from the historically limited availability of nest sites rather than from nest failure rates or food availability. Therefore, a consequence of the dependence on existing cavities may be selection for increased reproductive effort when a nest site is obtained (Martin and Li 1992, Martin 1995).

A recent paper by Collias (1997) argued that the diversity of nests built by passerine birds is a key to explaining the adaptive radiation of this avian group during the late Tertiary. Collias emphasized the importance of the flexibility in nest-site choice that accompanies the ability to build a variety of nest types, and linked this flexibility with the radiation of passerines into new niches. Another context in which flexibility in nest-site choice might be important is in the evolution of colonial nesting (e.g., Eberhard 1998), particularly among cavity-nesters, in which the evolution of social behavior may be affected by whether a species is an excavator or a cavity-adopter. For coloniality to evolve, one fundamental condition must be met: breeding pairs must be able to nest in proximity to other breeding pairs. Because they depend on pre-existing cavities, cavity-adopters have much less control over the location of their nests than do excavators, and the breeding densities of obligate cavity-adopters can be limited by the availability of nest sites (Brawn and Balda 1988). Flexibility and control over nest placement could allow gregarious nesting by making it easier for breeding pairs to build nests near conspecific pairs.

A comparative analysis of coloniality in birds has shown that coloniality is a relatively labile trait, and that it is correlated with the absence

of feeding territories, with aquatic habitat, and with nest exposure to predators (Rolland et al. 1998). There are several possible advantages to nesting in colonies, including access to and selection of favorable breeding sites, enhanced foraging efficiency, improved detection of and defense against predators, and access to breeding partners (Siegel-Causey and Kharitonov 1990). Breeding pairs probably use the presence or reproductive success of conspecifics as cues to indirectly assess the commodities necessary to breed (e.g., food, safety, health, mates, breeding sites), and then choose breeding sites that are near those of successful conspecifics (Danchin and Wagner 1997). However, even if the above factors favor gregarious nesting, coloniality can only result if nesting substrates are available in large enough patches to accommodate large groups. Because pre-existing cavities suitable for breeding are not likely to be dense, obligate cavity adoption might be expected to preclude the evolution of group nesting even if selection favored group nesting.

This paper examines the hypotheses that among cavity-nesting birds, excavators and cavity-adopters differ in their propensity to evolve colonial breeding, and that obligate cavity adoption tends to block the evolution of coloniality. I review data on the nest types and nest dispersion of several avian groups that include large numbers of cavity-nesting species, to examine the evidence that coloniality is unusual in cavity-adopting species. Recognizing the importance of taking phylogenetic relationships into account when testing this kind of evolutionary hypothesis, I also present a phylogeny-based comparative analysis of nesting behavior in the Anseriformes that tests the hypothesis that coloniality is unlikely to evolve among non-excavating cavity-adopters.

METHODS

I obtained information on nesting behavior from the literature, and followed Sibley and Monroe's (1990) taxonomic classification of birds in tallying the data. Rather than attempting to complete an exhaustive survey, I chose avian groups on the basis of two criteria: that they contain a substantial number of cavity-nesting species, and that published information on their nesting behavior be readily available. For each species in the groups examined, I collected the following data: nest type (open nest or cavity nest),

type of cavity-nester (excavator or cavity-adopter), and breeding dispersion (solitary or colonial). In species that were variable in a given character, the predominant character state was used (e.g., solitary nesters that occasionally form loose groups were coded as solitary). However, in cases where two character states appeared to be equally common in a species, the character was coded as polymorphic. Species for which data on both nest type and nesting dispersion were not available were omitted from the analyses. In addition, one duck species (*Heteronetta atricapilla*, Anatidae) was omitted, since it a brood parasite.

I chose to study Anseriformes because a complete genus-level phylogeny is available for the group, data on nesting are readily available, and the relatively large amount of variation in both nest type and nesting dispersion makes the group an ideal one for comparative analysis. Unlike most other avian orders, in Anseriformes both coloniality and cavity-nesting have arisen multiple times, providing a large enough sample size and power to conduct a statistical test. Using MacClade (Maddison and Maddison 1992), I redrew Livezey's (1986) phylogeny and expanded it by adding the corresponding species to the end of each genus branch. The node from which each genus-group of species emerged was coded as a soft polytomy. I then mapped two binary nesting characters onto the tree: nest type (0, nonexcavated cavity; 1, excavated cavity or open nest), and nest dispersion (0, solitary; 1, colonial).

I used two different comparative tests to evaluate the hypothesis that cavity adoption tends to block the evolution of coloniality. The first, MacClade's concentrated changes test (CCT; Maddison 1990), tests whether changes in a binary character (in this case the appearance of coloniality) occur more often than expected by chance in particular parts of the phylogeny (in this case, in lineages that are not composed of obligate cavity adopters). Since the CCT can only be applied to dichotomous trees, the anseriform tree was resolved arbitrarily using MacClade's random polytomy resolution function, and the test was repeated 100 times using 100 different randomly resolved trees. Probabilities were calculated using 1000 simulations with either ancestral state allowed. For each tree, I ran simulations examining actual changes, and also reconstructed changes (with both the

MINSTATE and MAXSTATE functions; see Maddison and Maddison 1992). The observed numbers of gains and losses in coloniality were obtained by mapping the dependent variable (nest dispersion) on the resolved tree; when necessary, ambiguity was resolved using the DELTRAN option. For each set of calculations, I recorded the probability of having as many or more than the observed number of gains in coloniality, and as many or more than zero losses.

Because the CCT only tests for a correlation, and not a cause-effect relationship between characters, I also tested the alternative hypothesis that obligate cavity-adoption is unlikely to evolve in colonial lineages. I performed the test using actual changes, repeating it 25 times using different randomly resolved trees (the test was not repeated more than 25 times, as it became clear that further repetitions would not yield a *P*-value that approached significance).

The second comparative test that I used to test the hypothesis that coloniality is more likely to evolve in lineages that are not cavity-adopters is Pagel's (1994) method for the comparative analysis of discrete characters. This method permits tests of hypotheses of correlated character evolution by comparing the fit of two maximum-likelihood models to the observed data, one that specifies independent evolution of the two characters, and the other that allows correlated evolution (comparison of the two models is called the "omnibus test"). When a model is fitted to the data, a set of transition rate probabilities is estimated; the parameters correspond to the state changes among the four states that are possible with two binary characters.

With this method, it is possible to test whether change in one character is contingent on the state of the other. This is done by forcing the relevant transition parameters to be equal, and then using a likelihood-ratio test (distributed as a χ^2 with 1 df) to compare the likelihood of this model to the free-parameter correlated evolution model. It is also possible to determine whether a transition parameter is significant by setting it equal to zero and comparing the resulting likelihood with the likelihood of an unrestricted model.

Unlike Maddison's CCT, Pagel's method takes into account branch lengths in the phylogenetic tree under consideration, and represents the reconstructed character states on the tree's internal nodes as probability distributions rather than a

TABLE 1. Taxa included in the survey of nesting behavior, and the numbers of cavity nesting and colonial species in each group. Sibley and Monroe's (1990) classification was used in tallying the data. The number of species indicates the number included in the analysis. References: (1) Cramp and Simmons (1997), (2) del Hoyo et al. (1992), (3) Frith (1967), (4) Forshaw (1989), (5) Fry et al. (1992), (6) Gaston and Jones (1998), (7) Marchant and Higgins (1990), (8) Gomez-Dallmeier and Cringan (1990), (9) Johnsgard (1978), (10) Kemp (1995), (11) Madge and Burn (1988), (12) Turner and Rose (1989), (13) Warham (1990), and (14) Winkler et al. (1995).

Order	Family	Number of genera	Number of species analyzed (excluded ^a)	Cavity nesters (adopters)	Colonial nesters	Colonial cavity nesters (adopters)	Reference
Struthioniformes	Apterygidae	1	3 (0)	3 (0)	0	0 (0)	7
Anseriformes	Anhimidae	2	3 (0)	0 (0)	0	0 (0)	2
	Anseranatidae	1	1 (0)	0 (0)	1	0 (0)	9
	Dendrocygnidae	2	9 (0)	3 (3)	0	0 (0)	2, 3, 8, 9
	Anatidae	39	129 (0)	22 (22)	12	0 (0)	1, 2, 11
Piciformes	Picidae	26	131 (83)	131 (2)	3	3 (0)	14
Bucerotiformes	Bucerotidae	8	54 (0)	54 (54)	0	0 (0)	10
	Bucorvidae	1	2 (0)	2 (2)	0	0 (0)	10
Coraciiformes	Coraciidae	2	10 (2)	10 (9)	0	0 (0)	5
	Alcedinidae	3	17 (7)	17 (0)	0	0 (0)	5
	Dacelonidae	9	33 (28)	33 (1)	0	0 (0)	5
	Cerylidae	3	7 (2)	7 (0)	0	0 (0)	5
	Meropidae	3	22 (4)	22 (0)	9	9 (0)	5
Psittaciformes	Psittacidae	66	231 (118)	230 (207)	3	2 (1)	4
Ciconiiformes	Laridae [Alcinae]	12	22 (1)	17 (13)	20	17 (12)	6
	Procellariidae	22	90 (24)	75 (5)	85	71 (0)	13
Passeriformes	Hirundinidae	14	78 (1)	44 (23)	16	6 (0)	12
Totals		214	842 (270)	670 (341)	149	108 (13)	

^a Number of species for which data on nest type or nesting dispersion were missing.

single set of inferred (parsimony or outgroup-based) values. For this analysis I used an anseriform tree for which polytomies had been randomly resolved by MacClade. Branch lengths among genera were coded following Livezey (1986) with one length unit per character change; internodes that had been formed by polytomy resolution were given a length of 0.1, and species branches were all given unit length. Since this method cannot handle polymorphic character coding, the few (4 of 149 taxa) cases of polymorphism were coded to reflect the ancestral character state (the state shared with the taxon's closest relative). A significance level of $P < 0.05$ was used for comparative tests using both the CCT and Pagel's method.

RESULTS

Information on nesting behavior from 842 species in 214 genera, spanning 17 bird families and 8 orders, was obtained from the literature (Table 1). Species for which data on both nest type and nesting dispersion were not available are not included in the above tally. A complete species-by-species listing of the survey results is

available from the author. Data from the survey are consistent with the hypothesis that colonial nesting does not tend to occur in lineages of cavity-adopters. In the above sample, 670 of 842 species (80%) are cavity-nesters and 149 of 842 (18%) breed colonially. One-hundred-eight of 842 species (13%) are colonial cavity-nesters, and except for one parrot and 12 auk species, these colonial cavity-nesters excavate their own nests. The only exceptions are the Maroon-fronted Parrot (*Rhynchopsitta terrisi*), which nests in cliff crevices at high densities (Forshaw 1989), and several auks, which use crevices in rock piles, cliffs, or talus slopes. All other colonial breeders either excavate their own nesting cavities or build their own nests.

There were only a few cases (not included in the previous 108) in which a primarily cavity-adopting species nests colonially under certain conditions. Bulwer's Petrel (*Bulweria bulwerii*, Procellariidae) has sometimes been found to nest at high densities using closely spaced crevices among rocks on islands (Warham 1990). Among the Anseriformes, the Fulvous Whistling-Duck (Dendrocygnidae: *Dendrocygna bicolor*) occa-

sionally nests in colonies, but when it does it builds a nest on the ground rather than occupying a cavity (Madge and Burn 1988); on small islands in Tamaulipas, Mexico, the Black-bellied Whistling-Duck (*Dendrocygna autumnalis*) nests at high densities on the ground (Markum and Baldassarre 1989); the Wood Duck (Anatidae: *Aix sponsa*) is sometimes loosely colonial if holes are available close together (del Hoyo et al. 1992); and the Red-breasted Merganser (Anatidae: *Mergus serrator*) is often a gregarious nester, but is not an obligate cavity-nester and often uses shallow depressions in the ground as well as hollows or crevices (Cramp and Simmons 1997), which allow it flexibility in nest placement. Five sister species of African lovebird (Psittacidae: *Agapornis personata*, *A. liliana*, *A. fischeri*, *A. nigrigenis*, and *A. roseicollis*) build cup or domed nests within cavities (Forshaw 1989), and it is likely that this nest-building permits the modification of otherwise unsuitable cavities, thereby giving breeding pairs increased flexibility in nest-site choice (Eberhard 1998). Three of these lovebird species (*A. personata*, *A. liliana*, and *A. roseicollis*) are known to be colonial (Forshaw 1989, Juniper and Parr 1998). Other parrots have been reported to nest gregariously when closely spaced cavities are available: *Glossopsitta porphyrocephala*, *Polytelis alexandrae*, *Lathamus discolor*, *Aratinga wagneri*, *Ognorhynchus icterotis* (Forshaw 1989), and *Ara militaris* (Rowley 1984). Furthermore, in a number of species descriptions, Turner and Rose (1989) indicate that aggregation of breeding swallows depends on the availability of clumped nest sites (e.g., *Stelgidopteryx ruficollis* and *S. serripennis*, *Tachycineta thalassina*, *Notiochelidon murina* and *N. cyanoleuca*, *Progne chalybea*, *Psaldoprocne fuliginosa*, and *Hirundo andecicola*). Similarly, in his book on petrels Warham (1990:187) notes that in *Oceanites*, *Garrodia*, and *Pelagodroma* "burrow densities may be high but those species using natural cavities under stones are restricted by availability of suitable niches." In sum, these exceptions support the hypothesis that among cavity-nesters, coloniality is associated with the ability to excavate cavities or construct a nest, and that the aggregation of cavity-adopters is dependent on cavity density.

Using Maddison's (1990) CCT, a comparative analysis of nesting behavior in the Anseriformes supported the hypothesis that obligate cavity

adoption tends to block the evolution of colonial breeding. Depending on the method used to calculate probabilities of obtaining the observed number of gains of coloniality, the occurrence of colonial breeding was significantly, or nearly significantly, different from the null expectation that the evolution of coloniality occurs at random with respect to nest type. When *P*-values were averaged over the 100 randomly resolved trees, the following means were obtained: $P = 0.06 \pm 0.06$ (SD) using actual changes; $P = 0.06 \pm 0.07$ using MINSTATE ambiguity reduction; and $P = 0.05 \pm 0.02$ using MAXSTATE ambiguity reduction. These values are probably conservative, since the concentrated changes test is susceptible to Type II error when the proportion of "white" branches (branches in which the independent character has a value of 0) is <20% (Lorch and Eadie 1999). In the case of the phylogeny tested here, 19% of the branches were white (cavity-adopter lineages).

An alternative hypothesis, that obligate cavity-adoption tends to be blocked by coloniality, was not supported. In this case the CCT did not indicate a significant association between cavity-adoption and solitary nesting (averaged over 25 randomly resolved trees, $P = 0.38 \pm 0.07$).

The likelihood-based comparative analysis of the full Anseriform dataset indicated that the evolution of nest type and nesting dispersion are correlated ($P < 0.05$). A contingent changes test suggested that the transition from solitary to colonial nesting is not contingent on nest type, and that the most likely transition is from colonial cavity-nesting to colonial open-nesting. However, this implies that the ancestors of colonial open-nesters are most likely to be colonial cavity-nesters. Given that colonial cavity-nesting is only observed under the unusual circumstances noted above (and was not included as a character state on any terminal nodes), the results of this initial analysis are difficult to interpret biologically.

An examination of the distribution of nest types and nesting dispersion on the phylogeny found that within the genus *Mergus*, two of the three species are solitary cavity-nesters (as are the nearest relatives) and the third species is a colonial open-nester, implying two character transitions over a very short branch. Since this could cause the corresponding transition parameter to be very large (M. Pagel, pers. comm.), the analysis was repeated with a phylogeny in

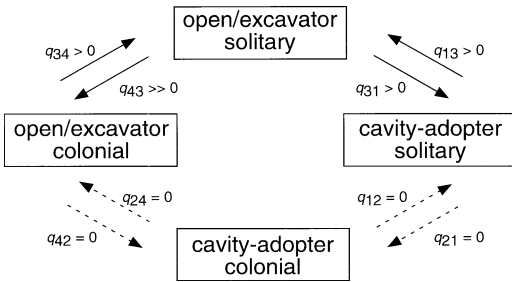


FIGURE 1. Flow diagram showing the transitions involved in the evolution of coloniality relative to nest types in Anseriformes. "Cavity-adopter" refers to non-excavating cavity-nesters, while "open/excavator" nesters are species that use open nests or excavate their own cavities. Transition rate parameters are denoted by q_{ij} , in which the subscripts indicate the combination of character states at the beginning (i) and end (j) of a given transition; possible character state combinations are 1 (0,0), 2 (0,1), 3 (1,0) and 4 (1,1). Solid arrows indicate pathways whose transition probabilities are significantly greater than zero according to alternative model tests (Pagel 1994); dotted arrows represent pathways that are not statistically significant.

which the above transition was removed (the three species of *Mergus* were coded as solitary cavity-nesters, resulting in one origin of coloniality fewer than in the previous analysis).

In this second analysis, the omnibus test again indicated that the two characters are correlated ($P < 0.03$; Fig. 1). The transition parameters were biologically more reasonable, with very low transition probabilities estimated for transitions involving the colonial cavity-nesting state. None of the contingent changes tests was significant, so the data did not show that the change in either of the characters is dependent on the state of the other. However, the appearance of coloniality in open-nesters was statistically significant, while the transition probability from solitary to colonial breeding in cavity-nesters was not significantly greater than zero. Like the CCT analysis, this is consistent with the hypothesis that coloniality is more likely to evolve in open-nesting (or excavator) species, and the lack of significance in the contingent changes test may be due to the relatively low number of changes in the two binary characters.

DISCUSSION

Taken together, the survey of nesting behavior across a wide taxonomic range of birds and the comparative analysis of nesting behavior in the Anseriformes indicate that colonial breeding is

unlikely to evolve among obligate cavity-adopters. The importance of nest-site choice in permitting coloniality is evident from the fact that for a number of taxa, gregarious nesting is contingent on the availability of closely spaced nesting sites. The evolution of coloniality is not a necessary consequence of the ability to excavate or build a nest (there are many excavators and open nesters that breed solitarily) but obligate cavity adoption does appear to limit the possibility of nesting close to conspecifics.

The facilitation of social nesting due to novel nest-building behavior has been previously documented for the swallows (Winkler and Sheldon 1993). However, instead of focusing on the nest-building or nest-site-choice hypothesis presented here, the authors argued that the evolution of dense coloniality in mud-nesting swallows occurred because the closed nest cup counteracted the increased chances of forced extra-pair copulations (EPCs) expected at high breeding densities. (An alternative interpretation, suggested by Wagner's [1993] hidden lek hypothesis, is that the pursuit of extra-pair copulations by females promotes aggregated nesting.)

As Collias and Collias (1984) have pointed out, coloniality in swallows is not only associated with the ability to build mud nests, but also with the ability to excavate burrows. Like nest building, nest excavation permits flexibility in choosing a nest site, evidently facilitating the evolution of colonial nesting. In addition to the colonial mud-nesters, the Bank Swallow (*Riparia riparia*), which is a burrow-nester, is strongly colonial (Turner and Rose 1989), and several of the cavity-adopting species included in the Winkler and Sheldon phylogeny occasionally nest in small groups, depending on the availability of cavities (Turner and Rose 1989). This does not invalidate either the EPC-avoidance hypothesis or the hidden lek hypothesis, but supports the idea that the evolution of a colonial breeding system is initially facilitated by the flexibility of nest placement that goes with building or excavating a nest.

In the context discussed in this paper, cavity nesting, in particular for cavity-adopters, appears to limit the choices available to breeding pairs in selecting a nest site. Nevertheless, some avian lineages show little variation in nest type, and there are large groups of birds composed almost entirely of cavity-nesters (e.g., Piciformes and Coraciiformes), and the parrots (Psit-

taciformes) are, with very few exceptions, all obligate cavity-adopters. The striking sociability of most parrots, juxtaposed with the fact that most species nest solitarily, led Ward and Zahavi (1973) to call them "suppressed colonial breeders." The persistence of cavity-nesting and roosting in otherwise ecologically and morphologically diverse groups has been discussed by Ligon (1993), and he suggests that several factors (inability to tolerate low temperatures, slow development times, high predation in tropical areas, and lack of fecal sacs) might account for the pattern.

The causes and consequences of nest-building behavior are complex, and although in many cases it is difficult to establish the directionality of cause-effect relationships, some general patterns are evident. There are strong associations between the type of nest used by a bird and its life-history characters (Martin 1995). The ability to choose nest sites, discussed by Collias (1997) in the context of moving into new ecological niches, could also affect the evolution of social behavior by facilitating gregarious nesting. This hypothesis is supported by a taxonomically broad survey of cavity-nesting birds as well as a comparative analysis of nesting behavior in the Anseriformes, both of which indicate that excavators are more likely than cavity-adopters to evolve colonial breeding systems, presumably because excavators have more flexibility in choosing the location of their nests.

ACKNOWLEDGMENTS

I thank Princeton University's Department of Ecology and Evolution and the Smithsonian Tropical Research Institute for support; and W. Eberhard, P. Grant, K. Harms, M. J. West-Eberhard, and anonymous reviewers for helpful comments and encouragement at various stages of the manuscript's preparation. Thanks also to M. Pagel who kindly made his analysis software available and answered questions about its implementation.

LITERATURE CITED

- BRAWN, J. D., AND R. P. BALDA. 1988. Population biology of cavity nesters in northern Arizona: do nest sites limit breeding densities? *Condor* 90:61–71.
- COLLIAS, N. E. 1997. On the origin and evolution of nest building by passerine birds. *Condor* 99:252–270.
- COLLIAS, N. E., AND E. C. COLLIAS. 1984. Nest building and bird behavior. Princeton University Press, Princeton, NJ.
- CRAMP, S., AND K. E. L. SIMMONS [EDS.]. 1997. Handbook of the birds of Europe, the Middle East and North Africa: the birds of the Western Palearctic. Oxford University Press, New York.
- DANCHIN, E., AND R. H. WAGNER. 1997. The evolution of coloniality: the emergence of new perspectives. *Trends in Ecology and Evolution* 12:342–347.
- DEL HOYO, J., A. ELLIOTT, AND J. SARGATAL [EDS.]. 1992. Handbook of the birds of the world. Vol. 1. Lynx Editions, Barcelona.
- EBERHARD, J. R. 1998. Evolution of nest-building behavior in *Agapornis* parrots. *Auk* 115:455–464.
- FORSHAW, J. M. 1989. Parrots of the world. 3rd ed. Landsdowne Editions, Chipping-Norton, Sydney.
- FRITH, H. J. 1967. Waterfowl of Australia. Halstead Press, Sydney.
- FRY, C. H., K. FRY, AND A. HARRIS. 1992. Kingfishers, bee-eaters and rollers. Princeton University Press, Princeton, NJ.
- GASTON, A. J., AND I. L. JONES. 1998. The auks. Oxford University Press, New York.
- GOMEZ-DALLMEIER, F., AND A. T. CRINGAN. 1990. Biology, conservation and management of waterfowl in Venezuela. Editorial Ex Libris, Caracas.
- JOHNSGARD, P. A. 1978. Ducks, geese and swans of the world. University of Nebraska Press, Lincoln, NE.
- JUNIPER, T., AND M. PARR. 1998. Parrots: a guide to parrots of the world. Yale University Press, New Haven, CT.
- KEMP, A. 1995. The hornbills: Bucerotiformes. Oxford University Press, New York.
- LIGON, J. D. 1993. The role of phylogenetic history in the evolution of contemporary avian mating and parental care systems. *Current Ornithology* 10:1–46.
- LIVEZEY, B. C. 1986. A phylogenetic analysis of recent anseriform genera using morphological characters. *Auk* 103:737–754.
- LORCH, P. D., AND J. MCA. EADIE. 1999. Power of the concentrated changes test for correlated evolution. *Systematic Biology* 48:170–191.
- MADDISON, W. P. 1990. A method for testing the correlated evolution of two binary characters: are gains or losses concentrated on certain branches of a phylogenetic tree? *Evolution* 44:539–557.
- MADDISON, W. P., AND D. R. MADDISON. 1992. MacClade: analysis of phylogeny and character evolution, v. 3.07. Sinauer Associates, Sunderland, MA.
- MADGE, S., AND H. BURN. 1988. Waterfowl: an identification guide to the ducks, geese and swans of the world. Houghton Mifflin, Boston.
- MARCHANT, S., AND P. J. HIGGINS. 1990. Handbook of Australian, New Zealand and Antarctic birds. Vol 1. Oxford University Press, Melbourne.
- MARKUM, D. E., AND G. A. BALDASSARRE. 1989. Ground nesting by Black-bellied Whistling-Ducks on islands in Mexico. *Journal of Wildlife Management* 53:707–713.
- MARTIN, T. E. 1995. Avian life history evolution in relation to nest sites, nest predation, and food. *Ecological Monographs* 65:101–127.
- MARTIN, T. E., AND P. LI. 1992. Life history traits of open- vs. cavity-nesting birds. *Ecology* 73:579–592.

- PAGEL, M. 1994. Detecting correlated evolution on phylogenies: a general method for the comparative analysis of discrete characters. *Proceedings of the Royal Society of London Series B* 255:37–45.
- ROLLAND, C., E. DANCHIN, AND M. DE FRAIPONT. 1998. The evolution of coloniality in birds in relation to food, habitat, predation, and life-history traits: a comparative analysis. *American Naturalist* 151: 514–529.
- ROWLEY, J. S. 1984. Breeding records of land birds in Oaxaca, Mexico. *Proceedings of the Western Foundation of Vertebrate Zoology* 2:73–224.
- SIBLEY, C. G., AND B. L. MONROE JR. 1990. Distribution and taxonomy of birds of the world. Yale University Press, New Haven, CT.
- SIEGEL-CAUSEY, D., AND S. P. KHARITONOV. 1990. The evolution of coloniality. *Current Ornithology* 7: 285–330.
- TURNER, A. K., AND C. ROSE. 1989. A handbook to the swallows and martins of the world. Christopher Helm, London.
- WAGNER, R. H. 1993. The pursuit of extra-pair copulations by female birds: a new hypothesis of colony formation. *Journal of Theoretical Biology* 163:333–346.
- WARD, P., AND A. ZAHAVI. 1973. The importance of certain assemblages of birds as “information centres” for food-finding. *Ibis* 115:517–534.
- WARHAM, H. 1990. The petrels: their ecology and breeding systems. Academic Press, San Diego, CA.
- WINKLER, H., D. A. CHRISTIE, AND D. NURNEY. 1995. Woodpeckers: a guide to the woodpeckers, piculets and wrynecks of the world. Pica Press, East Sussex, UK.
- WINKLER, D. W., AND F. H. SHELDON. 1993. The evolution of nest construction in swallows (*Hirundinidae*): a molecular phylogenetic perspective. *Proceedings of the National Academy of Sciences* 90: 5705–5707.