Manual of Parrot Behavior
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Many have forgotten this truth, but you must not forget it. You remain responsible, forever, for what you have tamed.

—Antoine de Saint-Exupery

Preface

The untamed beauty of parrots has fascinated humans for centuries and keeps us in its spell to the present time. Parrots are beautiful, they can fly, they are different from us, they are intelligent, and they remain mysterious. However, our relationship with parrots has changed greatly over time. Once considered a plentiful natural resource worth exploiting, we now make great efforts to protect their dwindling natural populations. At the same time we have come a long way in how we keep parrots in our homes. They no longer are but brilliant exhibition pieces chained to a T-stand but have become members of our families whose sensitivities, cognitive abilities, and emotions we respect and try to understand.

Yet parrot-keeping is a challenging endeavor. We admire their wildness, yet we bring them into a very unnatural captive environment for which they have not evolved. We admire their flight, yet in most cases where we keep parrots as pets we need to clip their wings. We like them because they are social creatures, yet we frequently keep them as solitary birds so they will redirect their affection toward us, and in most cases we leave them alone for extended periods of time. We recognize their intelligence, yet maintain them in a very restricted and confining environment.

No wonder behavior problems in parrots are plentiful and the numbers of abandoned parrots ending up in sanctuaries is increasing. Stories of parrots relegated to small cages in the basement, neglected, covered with a towel to keep them quiet, are much too common. Even normal parrot behavior such as vocalization, chewing, and being messy does not fit well with people’s lifestyles and can result in a broken human-animal bond. This book is written by authors who understand and love parrots in order to help foster a mutually beneficial and enjoyable relationship between parrots and their humans. We hope it can set up new parrot-human relationships for success and rekindle the joy that should be inherent in such relationships in cases where it has been lost. We intend to promote a deepened understanding and responsible attitude toward parrots in the wild as well as in captivity. We hope this will contribute to the welfare of parrots and help develop a respect for and appreciation of these fascinating beings.

Although scientific interest in parrot behavior is growing, knowledge in this area is still limited. This is especially true for behavior problems of pet birds and their treatment. The information in this book is based on scientific principles and available publications but, where specific and proven information is not available, may reflect the opinion and the personal experience of the authors. Therefore, there may be some degree of contradiction or difference in interpretation between chapters. This inconsistency was intentionally maintained to offer the reader different perspectives.
Manual of Parrot Behavior
1
Classification and Status of Wild Populations of Parrots

Dominique G. Homberger

THE ORDER PSITTACIFORMES AND ITS RELATIONSHIPS WITHIN THE CLASS AVES

The roughly 350 species in about 74 genera of parrots and cockatoos (Forshaw 1989; Collar 1997; Rowley 1997; Juniper & Parr 1998) are grouped within the Psittaciformes, one of the most distinctive and largest of the 28 avian orders (Brooke & Birkhead 1991). Parrot and cockatoo species are usually easily recognized as psittaciform (or “psittacine”) birds because of their curved beaks, in which the tip of the maxilla projects beyond the shorter mandible, and their zygodactylous feet, in which the second and third toes point forward and oppose the first and fourth toes, which point caudally. Other characteristics include a usually colorful plumage; a very large brain; curiosity, lifelong capacity for learning, and adaptability to changing environmental conditions; distinctive vocalizations; a feeding ecology as seed predators; versatile feeding mechanisms; a complex social behavior; lifelong pair bonding; nesting in cavities; white eggshells; and nidicolous young.

In the past, there have been some attempts at identifying the avian orders that are most closely related to the Psittaciformes by looking for common features, but it has become clear that any such commonalities reflect traits that have evolved in adaptation to similar environmental conditions and not traits that have been retained from a common ancestor. Furthermore, most of the common features at the ordinal level resemble one another only superficially and are easily recognized as having evolved independently in various avian orders. For example, in the curved beak of owls (Strigiformes) and raptors (Falconiformes), the mandible points straight forward, and the hooked maxilla serves to get a grip when grabbing or tearing apart prey. In the zygodactyl feet of woodpeckers (Piciformes) and cuckoos (Cuculiformes), the limb musculature differs from that of Psittaciformes, and the scaly skin differs in the shape and number of the scales. These differences indicate that the zygodactyl feet reflect an adaptation to an arboricole lifestyle, which has evolved separately in the ancestors of each order, rather than one that has evolved in a common ancestor of all three orders.

THE EVOLUTIONARY ORIGIN OF PSITTACIFORMES

The evolutionary origin of the Psittaciformes can be reconstructed from a combination of functional morphological, ecological, phylogenetic, biogeographical, geological, and paleoecological data (Cracraft 2001; Homberger 1991, 2003). The zygodactylous feet that are especially adept at climbing tree trunks and the predominant nesting in tree cavities suggest that the Psittaciformes originated as forest birds. The white color of the eggshells indicates that the ancestral species incubated their eggs in cavities (probably of trees), where they would not need camouflaging color pattern to escape the attention of predators.

The functional morphology of their feeding apparatus provides additional support for a psittaciform origin from an ancestor that was adapted to living in forests (Homberger 2003). The quadratomandibular, or jaw, joint is uniquely
shaped to allow lateral movements of the lower mandible relative to the upper maxilla. However, parrots and most cockatoos, such as the White and Pink Cockatoos (Cacatua spp., Eolophus roseicapillus, Lophochroa leadbeateri, Plicitolophus spp.), the Cockatiel (Nymphicus hollandicus), the Yellow-tailed and White-tailed Black Cockatoos (Calyptrorhynchus [Zanda]), and the Palm Cockatoo (Probosciger aterrimus), use this capacity only during bouts of bill honing and for minor adjustments when positioning food items between their mandible to bite into them. It is unlikely, therefore, that the psittaciform jaw articulation was evolved in conjunction with the bill movements observed in these species. It has long been suspected that it was a feature that originated in a psittaciform ancestor as part of a feeding behavior that differed from that which is common among extant parrots (Homberger 1981).

In contrast, the lateral deflection of the lower mandible is an integral part of the feeding mechanism in most Red-tailed Black Cockatoos (Calyptrorhynchus banksii subspecies), the Glossy Black Cockatoo (C. lathami), and the Gang-gang Cockatoo (Callocephalon fimbriatum) (Homberger 2001, 2003). They align one of the paired, projecting corners of their V-shaped lower bill tip with their upper bill tip. They do this in order to use their beak as pincer-like pliers to tear apart woody branches to extricate wood-boring or gallicole insect larvae or to break apart woody-fibrous capsules to extract seeds (Homberger 2001, 2003). These species also possess a bony suborbital arch that juts out on the sides of their skull and is firmly buttressed against the postorbital and zygomatic processes of the cranium. The jaw muscles that attach to this suborbital arch assume an orientation that emphasizes transversely directed force components, which are instrumental for the lateral deflections of the mandible during feeding in these species. In this “calyptorhynchid” feeding apparatus, the shapes of the jaw joint, skull, and bill are structurally and functionally integrated with the feeding mechanism to tear apart food sources that are made of fibrous wood, which are prevalent in a wooded or forested environment (Homberger 2003). The tight functional integration of the features of the calyptorhynchid feeding apparatus also indicates that they are part of an ancestral condition for Psittaci-formes. The calyptorhynchid feeding apparatus may have originated in a psittaciform ancestor first to extract wood-boring or gallicole insect larvae and subsequently been applied with few, if any, modifications, to extract seeds from fibrous-woody fruits.

In the “psittacid” feeding apparatus of parrots and most cockatoos (except the Red-tailed Black Cockatoos, Calyptrorhynchus lathami and most C. banksii subspecies, and the Gang-gang Cockatoo, Callocephalon fimbriatum), in contrast, the structure and function of the jaw joint does not fit the bill shape and feeding behavior. The psittacid feeding apparatus relies on specialized surface structures, such as the transverse step and filing ridges on the inside of the upper bill tip, to provide grip for seeds that are cut open with the cutting edge of the lower mandible (Homberger 1980a, 1980b, 2003). Psittaciforms with a psittacid bill (except the Pesquet’s Parrot, Psittrichas fulgidus) remove the shells of all seeds before swallowing them, and they do so with a stereotypical seed-shelling mechanism that does not require lateral movement of the mandible. During this seed-shelling procedure, the tip of the tongue places and holds a seed against the corrugated upper bill tip and its transverse step, while the cutting edge of the mandible cuts open the seed-shell. The bony suborbital arch is generally absent so that the transverse component of the jaw muscles is much reduced in favor of the longitudinal and vertical force components. If a suborbital arch is present, as in many South American species, it is less massive and fused only with the postorbital process of the cranium (see Smith 1975). This functional dissociation of the various structural and functional features indicates that the shapes of the jaw joint, skull, and bill of parrots and cockatoos with a psittacid feeding apparatus have changed under the influence of a variety of selective regimes arising from environmental conditions that differ from those to which the psittaciform ancestor was adapted.

The most significant selective advantage of the psittacid feeding apparatus over the calyptorhynchid feeding apparatus is that the former can use both sides of the jaw musculature simultaneously to maximize the bite force of the mandible. This selective advantage, however, can be utilized only in environments in which plants with seeds enclosed in fruits that are not woody-
fibrous predominate (Homberger 2003). Most of these fruits have a sclerotic endocarp (i.e., “stone”) that can be split, or cracked open, by applying a focused pressure, such as by the cutting edge of the mandible, onto their preformed weak points or sutures that facilitate the germination of the seeds. The selective advantage of a psittacid feeding apparatus appears to be considerable because it has evolved multiple times in separate lineages of parrots and cockatoos, including among them some of the populations and subspecies of Red-tailed Black Cockatoos (*Calyptorhynchus banksii*). This convergent evolution of the psittacid feeding apparatus is made evident by the great variability of the individual components and features, such as the pattern and configuration of the filing ridges and corneous palate, the shape and expression of the transverse step, the shape of the cutting edge of the mandible, and the configuration and degree of the reduction of the suborbital arch (Homberger 1980a, 1980b, 2003).

The large brain of the Psittaciformes earned them the epithet “avian primates.” As in primates, it is correlated with curiosity and exploratory behaviors and a lifelong capacity for learning (e.g., Mettke-Hofmann et al. 2002; Pepperberg 2002). This high degree of encephalization supports the hypothesis that the Psittaciformes originated from ancestors that were feeding on stationary food items that were hidden from sight (i.e., wood-boring or gallicole insect larvae and seeds within fruits) and, therefore, need to be located through indirect evidence and learning from experienced individuals. These arboreal food items further support the hypothesis that Psittaciformes originated in a forested environment.

Psittaciformes are concentrated in the continents and islands of the Southern Hemisphere with only limited expansions into the adjacent northern regions. Contrary to general impressions, Psittaciformes are not restricted to tropical regions, as several species occur in the colder regions of China, New Zealand, New Guinea, Tasmania, and South America. Such a distribution pattern can be understood only on the basis of past geological events. Biogeography has been suggestive of a psittaciform origin in the Southern Hemisphere (Boetticher 1959; Forshaw 1989) even before geological data could demonstrate that the southern continents were formed through the disintegration of the Mesozoic southern continent called Gondwana and their subsequent migration northward toward the equator (Frakes & Vickers-Rich 1991; Schodde & Tidemann 1986; Stevens 1991).

Gondwana’s climate in the Cretaceous was generally temperate to subtropical, and Gondwana itself was covered mostly with evergreen mesic forest and rain forest (White 1990). As the continents moved northwards, they tended to become more arid with the rising temperatures (Frakes & Vickers-Rich 1991; Stevens 1991; White 1994). The original plant communities that included southern gymnosperms (e.g., *Araucaria*), Casuarinas, Proteaceae (e.g., *Banksia*, *Protea*, *Grevillea*), Myrtaceae (e.g., ancestors of *Eucalyptus*), Podocarpaceae, Nothofagaceae (e.g., Southern beeches—*Nothofagus*), and so forth, adapted to the changing conditions, were replaced by other plant communities, or retreated to refugia in which the original Gondwanan conditions were retained or changed but little. Such Gondwanan refugia are found today in Australia along its eastern coast, the southeastern and southwestern corners, and in Tasmania; in New Zealand, New Caledonia, and Fiji; in the central highlands of New Guinea; in the Drakensbergs of eastern South Africa; and in the Valdivian and Patagonian rain forests along the eastern coast of southern South America and the cooler Atlantic rain forests in Southern Brazil.

In Australia, several of these seed plants (e.g., Casuarinas, Proteaceae, Myrtaceae) occur predominantly in the Gondwanan refugia (Schodde & Tidemann 1986) and bear complex inflorescences that mature into multi-seeded, fibrous-woody infructescences, called cones, cobs, or capsules. Several species have also become serotinous (i.e., they retain their mature fibrous-woody fruits for several years in their canopy instead of shedding their mature seeds), presumably in adaptation to their fire-prone environment (Homberger 2003). That the psittaciform species that possess a calyptorhynchid feeding apparatus (most Red-tailed Black Cockatoos, *Calyptorhynchus banksii* subspecies; the Glossy Black Cockatoo, *C. lathami*; and the Gang-gang Cockatoo, *Callocephalon fimbriatum*) not only occur in these refugia but also have a feeding apparatus that is specifically adapted to exploiting these plants supports the hypothesis that the calyp-
torhynchid feeding apparatus is the ancestral condition for Psittaciformes.

In the other southern continents and islands, the Gondwanan refugia are dominated by Gondwanan plants whose seeds are enclosed in thinner seed-shells (e.g., Araucariaceae, Nothofagaceae, some Podocarpaceae) or sclerotic endocarps with preformed weak points and sutures (e.g., some Podocarpaceae). The psittaciform species that feed on these seeds and are restricted to Gondwanan refugia can be surmised to have evolved their psittacid feeding apparatus already in adaptation to these plants before the breakup of Gondwana and were able to retain it because their environment changed little, if at all. This is probably the situation, for example, of the Austral and Slender-billed Conures (*Enicognathus ferrugineus* and *E. leptorhynchus*) in southern South America; the Vinaceous Amazon (*Amazona vinacea*) in southern Brazil; the Cape Parrot (*Poicephalus r. robustus*) in southeastern Africa; and the non-cacatuid psittaciforms with a psittacid feeding apparatus in the Australo-Pacific region.

The greatest diversity of Psittaciformes at the familial and subfamilial levels is found in the Australo-Pacific region (see Figure 1.1). This indicates that this part of Gondwana may have contained the greatest psittaciform diversity even before its separation from the remainder of Gondwana and further breakup into what is known today as Australia, New Guinea, New Zealand, New Caledonia, and Fiji.

**THE SUBDIVISION AND CLASSIFICATION OF THE PSITTACIFORMES**

The very ease with which psittaciforms can be identified as such is compensated by the difficulties that are encountered trying to subdivide this large order into smaller, hierarchically arranged taxonomic units that are united by common characteristics (i.e., families, subfamilies, tribes, genera). Such a classification creates order within the multitude of species, which is needed for scientific research (e.g., systematics, comparative morphology, evolutionary biology) and applied biology (e.g., evaluation of susceptibility to certain diseases, choice of foster parents for the management of endangered species). However, it must be kept in mind that every classification is only a hypothesis that needs to be tested continuously as new data emerge and earlier interpretations are re-evaluated in light of new observations. Changes in the nomenclature of taxa and in the hierarchical levels of taxonomic subdivisions are, hence, reflective of intense scientific activity but are not an end in themselves.

Numerous classifications have been proposed over the last 200 years, but all have faced considerable difficulties. One of the underlying reasons for this situation is that the Psittaciformes represent a very old group that had to adapt to numerous environmental changes in the course of its long history dating back to the early Tertiary (ca. 60 million years ago). Because similar environmental changes (e.g., aridification, tropicalization, colonization of volcanic islands, etc.) have occurred in different regions, many derived features have been acquired independently and convergently by different psittaciform lineages in adaptation to these new environments. This prevalence of convergent (i.e., homoplastic) features among the Psittaciformes as a group has hampered earlier efforts in classifying this avian order, mainly because many convergent and other non-homologous features have been misidentified as homologous ones that would indicate evolutionary relationships (for discussions, see Homberger 1980a, 1991; Güntert 1981).

The distinction between homologous and convergent features is one of the most challenging tasks for evolutionary biologists, because the first step in this procedure requires the analysis of both the structure and function of the features, as well as their biological role in the natural environment. Two examples will illustrate the basic approach. The first example will use the bony suborbital arch to demonstrate the possible pitfalls in analyzing features in isolation. A recent functional-anatomical analysis of the bony suborbital arch in cockatoos revealed that it is a component of the feeding apparatus and as such cannot be used as a feature in isolation. It also revealed that its most complete configuration is intimately connected with lateral mandibular movements during feeding in Black Cockatoos that possess a calyptorhynchid feeding apparatus. Various configurations of less complete suborbital arches in different psittaciform lineages that possess a psittacid feeding apparatus can, therefore, be interpreted as derived remnants of the ancestral condi-
Figure 1.1. Phylogram of psittaciform genera based conservatively on established criteria.
tion that is still present in psittaciforms with a calyptorhynchid feeding apparatus. This reinterpretation of the evolutionary history of the bony suborbital arch is contrary to the original interpretation by Hofer (1950, 1953) and Zusi (1993), both of whom did not have access to observations of psittaciforms in their natural environment.

The second example will use the oral plate of the upper rhamphotheca (i.e., corneous sheath of the maxilla) to demonstrate that a particular structure may be composed of several features that provide different insights for the reconstruction of the evolutionary history of the Psittaciformes. The oral plate of the upper rhamphotheca consists of three parts: The inside of the upper bill tip, the transverse step, and the corneous palate. The inside of the upper bill tip of parrots that possess a psittacid feeding apparatus is corrugated by filing ridges. These filing ridges, however, are arranged in patterns and are formed by the underlying soft tissues in a manner that is highly variable among, but generally characteristic of, species. The inside of the upper bill tip of psittaciforms that possess a calyptorhynchid feeding apparatus is smooth and lacks any surface structure (Homberger 2003). The evolutionary transition from the ancestral to the derived condition of the inside of the upper bill tip is modeled by the various populations and subspecies of the Red-tailed Black Cockatoo (Calyptorhynchus banksii) and is clearly correlated with the derived seed-shelling behavior of psittaciforms with a psittacid feeding apparatus (Homberger 2003). In contrast, the surface structure of the corneous palate, which is the feature with the greatest diagnostic value for the identification of genera in psittaciforms, does not have any functional significance (Homberger 1980a).

Mosaic evolution, that is, the presence of primitive and derived characters in a single species as a result of asynchronous evolutionary changes, has been another source of difficulties for the classification of the Psittaciformes. Because of it, a phylogeny that is based on a particular set of features, such as the feeding apparatus, may not simply correspond to another phylogeny that is based on a different set of features. As a consequence, the evolutionary history of each lineage and species needs to be reconstructed by carefully analyzing, weighing, and integrating a variety of data and observations. A simplified example taken from the Cacatuidae may illustrate such a case. Among birds in general, a large body size is a derived character, because flight has a much greater safety margin in small birds than in larger birds and, therefore, has probably originated in small avian ancestors whose flight apparatus may not have been perfected yet (Homberger & de Silva 2000; Homberger 2003). According to this criterion, the Cockatiel (Nymphicus hollandicus) could be considered the most ancestral cockatoo. This interpretation could be supported by its dark plumage color and pattern, which are similar to those of the Black Cockatoos (Calyptorhynchus spp.) and clearly more ancestral than the plumage colors and patterns of the White and Pink Cockatoos. But the Cockatiel’s psittacid feeding apparatus and its ecology in Australia’s more arid woodlands indicate that it has also acquired derived characters in adaptation to the aridification of Australia. In contrast, the Red-tailed Black Cockatoos and the Gang-gang Cockatoo are characterized by ancestral plumage colors and patterns and by the ancestral calyptorhynchid feeding apparatus. At the same time, the Red-tailed Black Cockatoos are among the larger cockatoos, whose body size may have evolved in conjunction with their more massive bills to handle their diet of large fibrous-woody fruits (Homberger 2003).

At this point in time, the best classification of the Psittaciformes may be one that is based on a large number of features, whose biological and evolutionary significance has been analyzed and is well understood. Unfortunately, we are still far from this goal. The proposed classification (see Figure 1.1) is presented as a pragmatic proposal that combines simplicity and familiarity and avoids some of the errors of earlier classifications.

THE STATUS OF WILD POPULATIONS OF PARROTS

Over the millions of years since their origin in the early Tertiary, many psittaciform species have survived and continued to adapt successfully to changing environmental conditions, as we can conclude from their present geographical distribution and the number of existing species and individuals. Other species have not been able to do so and have become extinct, as we know from historical records or from fossils in regions, such as Europe, in which psittaciforms have been absent in historical times. Rates of extinction are
difficult to estimate from the fossil record, because fossilization is a rare event in any case and especially so for organisms, such as the ancestral and many other Psittaciformes, that are relatively small and live in microorganism-rich forest environments with their characteristically rapid degradation of organic materials. Nevertheless, the large number of species that are known to have existed at least until the more recent rash of extinctions testifies to the success and probably net increase in number of species and individuals of the Psittaciformes over the course of their evolutionary history.

Although extinctions of species are a normal part of biological evolution, extinction must be counterbalanced by speciation, that is, the appearance of new species, if a taxon, or group of species, as a whole is to survive. The appearance of new species, however, is presently not occurring any longer, at least not naturally. This process normally starts when a certain portion of a population becomes separated from the rest of the population by the appearance of a geographical barrier, such as a river having changed direction, an area having been divided by the uplifting of a mountain or the formation of a desert, or a number of individuals having migrated permanently to an island. This separation, or isolation, prevents the exchange of genetic materials between the separate populations and provides the conditions for the two populations to accumulate distinctive mutations, undergo distinctive selective processes, and, thereby, acquire distinctive traits simply by themselves or in adaptation to distinct environmental conditions.

The main reason for natural speciation not to be initiated any longer is the accelerating and well-documented shrinking of the natural habitats, so that psittaciform populations cannot expand and subsequently be subdivided into non-interbreeding populations. However, the recent successful establishment of self-sustaining parrot populations from aviary and transport escapes in various urban and suburban places in regions that had been devoid of natural populations of psittaciforms may be considered an experiment in human-induced speciation. As we can extrapolate from earlier such experiments in the late 18th and early 19th centuries, during which European songbirds (e.g., House Sparrows, Starlings, Chaffinches, Blackbirds, European Goldfinches) were transported to colonies in North America, Australia, and New Zealand by homesick European emigrants, the successful psittaciform expatriate populations in Germany, England, and North America may eventually become genetically distinct from their source populations. But modifications of external features will take many generations to become noticeable, as they did in the various domesticated psittaciforms, and these changes may reflect adaptations to the new environments or the lack of specific selection pressures (e.g., in cases of variable plumage colors), unless these mostly urban populations will be repeatedly swamped by new escapees and accidental releases. The possibility of such artificial speciation events may be a consolation, but hardly a compensation for the current progressive loss of the amazing diversity of psittaciform species in their natural environment.

There is no denying that the single-most threat to natural populations is the capture of individuals for aviculture and the pet market. Captive breeding of parrots by private individuals for conservation purposes should be recognized as the smoke screen that it is (Beissinger et al. 1991; Beissinger 2001; Snyder et al. 1997; Wright et al. 2001). Only a single psittaciform species, the Puerto Rican Amazon (Amazona vittata) (Wilson et al. 1994, Wunderle et al. 2003) has been brought back from the brink of extinction, which was made possible only through the lavish investment of governmental funding. The success of other governmental rescue programs for the Kaka (Nestor meridionalis) and Kakapo (Strigops habroptilus) in New Zealand (Beggs & Wilson 1991; Lloyd & Powlesland 1994) and the Orangebellied Parrot (Neophema chrysogaster) in Australia (Drechsler 1998) is still uncertain. Such massive financial investments for the rescue of single species are beyond the possibilities of even very wealthy persons. Furthermore, although there have been successful reintroductions of captive individuals into the wild provided that these could be integrated with natural populations of the same species (Brightsmith et al. 2003), simple releases of captive-bred psittaciforms into natural environments, whose resources are characteristically seasonal and unpredictable, have not been successful (Snyder et al. 1994). The reason for these difficulties may well be based in the evolutionary origin of the Psittaciformes with their spec-
cialized diet of wood-boring and gallicole insect larvae, which could be detected only through indirect evidence and through learning from experienced individuals.

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Research on the behavioral characteristics of selected wild psittacines may be important in establishing management and conservation guidelines for these species, both in the wild and in captivity. An understanding of such behavioral characteristics may also have wider significance in aiding the interpretations of behavioral and natural history parameters in other psittacine birds. Prior to the 1970s, intensive biological studies of wild Neotropical parrots were nearly nonexistent. This gap in ornithological knowledge is now being rapidly remedied with numerous species under investigation throughout Central and South America and the West Indies. Yet to date there have been few attempts to integrate the information from various studies into coherent frameworks of biological understanding. In this offering, we provide a number of preliminary hypotheses about parrot behavior, based largely on studies of a variety of species, mainly in the genera *Amazona* and *Rhynchopsitta*. These hypotheses appear to have wide explanatory power, yet need to be tested in additional genera and species before their validity can be considered firm.

Our basic approach is the comparative one, looking at features of behavior that vary among species and attempting to correlate these differences with underlying ecological imperatives faced by the species under consideration. As raw materials for these comparisons, we rely heavily on intensive studies of (1) the Puerto Rican Parrot (*Amazona vittata*) by Snyder et al. (1987); (2) various subspecies of the Cuban Parrot (*Amazona leucocephala*) by Gnam (1991), Wiley (unpublished), and others; (3) the Hispaniolan Parrot (*Amazona ventralis*) by Wiley (unpublished); (4) the Jamaican Black-billed and Yellow-billed Parrots (*Amazona agilis* and *collaria*) by Koenig (1999); (5) the St. Lucia Parrot (*Amazona versicolor*), the Imperial Parrot (*Amazona imperialis*), the Red-necked Parrots (*Amazona arausiaca*) of the Lesser Antilles by Snyder, Koenig, and many others (unpublished); and (6) three species of amazons in northeastern Mexico by Enkerlin-Hoeflich (1995, unpublished)—the Red-crowned Parrot (*Amazona viridigenalis*), the Yellow-headed Parrot (*Amazona oratrix*), and the Red-lored Parrot (*Amazona autumnalis*). Studies of *Rhynchopsitta pachyrhyncha* and *terrisi* have been primarily carried out by Enkerlin-Hoeflich (unpublished), Cruz-Nieto et al. (1998), Snyder et al. (1999), Lanning and Shiflett (1981, 1983), and Lawson and Lanning (1982).

The particular behavioral features we consider here are (1) the values of intraspecific sociality in various species, (2) timing of nesting seasons, (3) site and pair fidelity, and nest reuse, (4) feeding behavior and rates, (5) relationships of species conspicuousness and nest accessibility to exploitation in the pet trade, and (6) deficits in breeding effort.
BACKGROUND

As generally understood, the genus *Amazona* includes 31 extant species limited largely to tropical areas of the Western Hemisphere. The various species occur from Argentina and Chile north through virtually all of mainland South America and Central America to northern Mexico (Juniper & Parr 1998). Feral populations of several species also exist in a number of southern cities of the United States, Mexico, and Puerto Rico (Enkerlin-Hoeflich & Hogan 1997; Mabb 1997). The West Indies have a particularly good *Amazona* fauna with nine extant species about evenly divided between the Greater Antilles and Lesser Antilles. Many *Amazona* species are now endangered, and most all are declining, threatened mainly by bird trade and habitat changes, but also in some cases by hunting, introduced exotic species, and other factors (Snyder et al. 2000). The various species of *Amazona* are far from monolithic in their behavior and ecology. Species vary in clutch and brood sizes, diets, feeding rates, degrees of sociality, reproductive effort, and reproductive success, to name just a few facets of interest.

The genus *Rhynchopsitta* has only two living species, both distributed in the highlands of northern Mexico in more or less “island-like” forest habitats. The Thick-billed Parrot (*R. pachyrhyncha*) is a tree-cavity nester inhabiting the Sierra Madre Occidental in western Chihuahua and eastern Sonora south through the mountains of Durango, Sinaloa, Nayarit, and Jalisco to Colima and Michoacan. It was also formerly a regular inhabitant of extreme southeastern Arizona and probably bred there until the early 20th century, although no historical records of nests exist for this region. The Maroon-fronted Parrot (*R. terrisi*) is a cliff-cavity nester that occurs in the Sierra Madre Oriental of northeastern Mexico in southeastern Coahuila, central western Nuevo León, and southwestern Tamaulipas (Juniper & Parr 1998). Like many of the *Amazona*, both extant species of *Rhynchopsitta* are globally threatened. In addition, on the basis of fossils, Rea (1997) recently described a third species of *Rhynchopsitta* (*R. phillipsi*), now extinct, that was apparently sympatric with both *pachyrhyncha* and *terrisi* in the Sierra Madre Oriental in the late Pleistocene. The former sympatry of *pachyrhyncha* and *terrisi* makes it quite clear that these two parrots are distinct species and not simply races of a single species, as they were considered by Forshaw (1990).

VALUES OF SOCIALITY AMONG *AMAZONA* AND *RHYNCHOPSITTA* PARROTS

In general, *Amazona* parrots tend to be highly social in foraging and roosting habits and somewhat social in nesting habits, but some conspicuous differences exist among species in these tendencies. Four species that stand out in their disinclination to travel in groups larger than family groups are the large amazons of the Lesser Antilles—the St. Lucia Parrot, the St. Vincent Parrot (*A. guildingii*), the Imperial Parrot, and the Red-necked Parrot. Although these species sometimes assemble in groups larger than family units at roosts and at rich food sources, they normally nest in relatively dispersed arrays and travel only as singles, pairs, or small family groups in moving from nests or roosts to foraging areas. In contrast, other amazons, including most of those in the Greater Antilles and Mexico, show clear tendencies toward clumped nesting, often travel in much larger groups, and typically feed in large aggregations. Low sociality in the Lesser Antillean species is also reflected in the fact that male and female adults often separate in foraging activities in the breeding season and often feed their young independently. Such independent provisioning of nests is virtually unknown in amazons of the Greater Antilles and the mainland Neotropics.

Are there any obvious ecological correlates to explain the relatively low sociality of the large amazons of the Lesser Antilles? One promising possibility is the fact that these species, essentially alone among species in the genus, live in habitats that are effectively free of predation threats from large raptors. Whereas most Greater Antillean amazons and essentially all mainland *Amazona* have to deal with threats from large raptors such as Red-tailed Hawks (*Buteo jamaicensis*), Peregrine Falcons (*Falco peregrinus*), and various *Accipiter* species, no large accipiters or buteos occur in the Lesser Antilles, and the Peregrine Falcons of these islands are largely wintering birds utilizing coastal areas separate from the rain forest habitats occupied by the Lesser Antillean parrot species.

The largest raptor in parrot habitats of most of
the Lesser Antilles is the Broad-winged Hawk, which is too small to represent a credible threat to the parrots and for which there are no records of parrot predation. The Red-tailed Hawk, on the other hand, is not a species to be underestimated in its capacities to take Amazona parrots. Records exist of it successfully dispatching a variety of Amazona and Rhynchopsitta species in the Greater Antilles and on the mainland.

Thus, to the extent that conspicuous flocking behavior has often been suggested as primarily an adaptation to reduce risks of avian predation, the Lesser Antillean amazons might be expected to gain little by flocking behavior and the tendency may never have evolved or may have disappeared in the evolutionary history of these species because of very low predation threats. Flocking behavior has often been envisioned as primarily a means to reduce predation via the increased vigilance possible when the combined sensory capacities of multiple individuals are available and when specific individuals can serve as sentinels for groups (see discussions in Snyder et al. 1987 and Yamashita 1987).

Only one of the Greater Antillean amazons shows social behavior similar to that of the Lesser Antillean species, the race of the Cuban Parrot on Cayman Brac (Amazona leucocephala hesterna). Like the Lesser Antillean species, the Cayman Brac Parrot rarely travels in groups larger than family groups, and its male and female adults often feed their young independently (Wiley, unpublished). And like the Lesser Antillean species, and as one might predict from the preceding discussion, this parrot lives in an environment free of significant avian predators. No Red-tailed Hawks or large accipiters occur on Cayman Brac, and the Peregrine Falcons that are seen there occasionally are mostly on the coast, posing no significant risks to the parrots.

The associations of low sociality with low predation risks and high sociality with high predation risks strongly suggest a causal connection of these features. Further reinforcing this conclusion is the fact that the race of the Cuban Parrot on Grand Cayman (Amazona leucocephala caymanensis) shows the typical Amazona tendency toward large flocks and apparently feeds its young as pairs. Significantly, there are Red-tailed Hawks on Grand Cayman, unlike nearby Cayman Brac. Thus the parrots of the various Cayman Islands in themselves give strong evidence for the importance of avian predators in producing social tendencies among Amazona parrots.

We also call attention to the especially well-developed sociality of the Thick-billed and Maroon-fronted Parrots of Mexico. These Rhynchopsitta species are similar to the amazons in size and face predation risks from the same sorts of avian predators. In particular, these species face significant predation threats from both Red-tailed Hawks and Peregrine Falcons, and in the case of the Thick-billed Parrot, also from Apache Goshawks (Accipiter gentilis apache). In our experience, sociality in the Rhynchopsitta species is even more highly developed than in any Amazona species for which we have data. In fact, pairs of the Thick-billed Parrot often nest very close together, sometimes with more than one pair in the same tree, while Maroon-fronted Parrots typically nest in dense colonies in cliffs. Moreover, observations indicate that breeding males of the Thick-billed Parrot typically associate in combined flocks for foraging, often waiting for one another to leave the nesting areas as a group. Such coordinated male behavior has not been regularly recorded for any Amazona species.

Other explanations for the flocking and sociality of amazon parrots—for example, traditional arguments for advantages in food finding in birds (see Krebs 1974)—have difficulty in accounting for the variations in sociality seen in various Amazona species. That there might be any basic differences in food availability for the Cayman Brac Parrot and the Lesser Antillean species that could explain their low sociality is undocumented and does not seem intuitively likely. Available evidence suggests that they feed on much the same foods that are taken by other more social species in the genus.

Regardless of what factors are truly most important in producing the relatively high degree of sociality found in most Amazona and Rhynchopsitta, this characteristic is generally considered to be adaptive in the lives of these species. Modern circumstances, however, can produce situations where this is clearly not true. We call attention to a recent instance of mass drowning of Rhynchopsitta terri in an artificial water catchment where the species suffered a major population stress precisely because of its high degree of sociality. In this instance, in 1994, at least 52 R.
terrisi perished when they were unable to exit from an artificial cement water tank that they had apparently entered for drinking and/or bathing purposes. When one considers that the total population of this species is only about 3,000 birds and the annual recruitment of young is only about 200 individuals, this event was nothing short of catastrophic (Macías-Caballero et al. 2001).

As an aside, Rhynchopsitta parrots, like many species of Australian parrots, but unlike most Neotropical parrots inhabiting humid environments and consuming foods high in water content, come to water sources, such as waterfalls, to drink on a daily basis. This behavior has been documented in both species of Rhynchopsitta (Snyder et al. 1999; Macías-Caballero et al. 2001), and, like the parrot assemblages at clay licks of the Amazon basin, constitutes a marvelous spectacle. Unfortunately, man-induced changes in the environment have both reduced the availability of springs and waterfalls in the landscape and increased the presence of artificial water catchments that can pose inadvertent risks of mortality to the species.

Another species for which high sociality may have led to major population stress from human sources is the extinct Carolina Parakeet (Conuropsis carolinensis). Flocks of this species were exceedingly vulnerable to shooting, and the tendency of the species to roost together in large groups in hollow trees made it susceptible to heavy harvest for the pet trade, both of which factors were of presumed importance in the species’ decline (Snyder & Russell 2002). The high sociality of this species may also have rendered it highly susceptible to the spread of exotic diseases.

Finally, as another aside, we note that the absence of any strong tendency for flocking in the Lesser Antillean and Cayman Brac Amazona is a factor that makes censusing of these species especially difficult. Although counts of large flocks entering and leaving roosts have proven an effective way to census many other Amazona species—for example, the Puerto Rican Parrot and the Bahama Parrot (A. leucocephala bahamensis)—it is not a practical option for species with low flocking tendencies.

**TIMING OF NESTING SEASONS**

In the West Indies, most amazon parrots begin egg laying in the late winter and early spring, with March usually the peak month. This timing is in general correlated with the dry season, and could be related primarily to minimizing risks of nest loss to flooding, although it could alternatively be keyed to seasonal aspects of food availability. Strongly suggesting the latter is the abnormally late egg-laying period seen in the Bahama Parrots of Abaco, which do not normally lay until late May and early June, just before onset of the rainy season in that region (Gnam 1991). Here, laying appears to be timed to take advantage of the abundance of poisonwood (Metopium toxiferum) fruits, wild guava (Tetrazygia bicolor) fruits and appropriate-aged pine (Pinus caribea) seeds in midsummer, the most important known foods for the species in provisioning young. The Bahama Parrots on Inagua Island apparently lay at a more typical time in the early spring, in line with other amazons of the West Indies (Snyder et al. 1982). Pine is absent from Inagua, and poisonwood is not nearly as conspicuous an element of the flora on this island as on Abaco.

Breeding seasons of mainland amazons have been especially closely studied in northeastern Mexico (Enkerlin-Hoeflich 1995) and are similar to most West Indian amazons, with peak laying in late March and early April (Table 2-1). The sympatric Red-crowned Parrot, Yellow-headed Parrot, and Red-lored Parrot have similar egg-laying dates. Food is abundant during spring and summer for Mexican Amazona. There is no clear-cut dry season, although spring and summer usually show peaks in rain and winter is normally dry. Their breeding season is earlier as one moves south and would indicate that it is more related to photoperiod or temperature than to food availability (Enkerlin-Hoeflich 1995, unpublished data).

Breeding seasons of the Rhynchopsitta species are extremely delayed relative to the Amazona species, and this delay is almost surely keyed to their specialized diets, primarily of various conifer seeds, which do not normally become abundantly available until midsummer, with early June being the low point in seasonal availability of seeds for the conifer species in the ranges of the species. The mean egg-laying date of the Thick-billed Parrot in Chihuahua has been mid-July, with most chicks fledged by the first or second week of October (Snyder et al. 1999). The Maroon-fronted Parrot starts somewhat later with
most egg-laying in late July to early August and chicks fledging at the end of October through the first week of November.

Thus, the evidence for importance of diet in determining the timing of breeding is highly suggestive both in the Bahama Parrot and the Rhynchopsitta parrots, and diet may be the most important factor with the other Amazona as well, although this is less clear from available data. Future studies focused on crop sampling of nestlings of a variety of species to rigorously determine dietary relationships (Enkerlin-Hoeflich et al. 1999), combined with studies of seasonal availability of primary foods, may help solidify knowledge of the most important factors determining the timing of breeding.

### Table 2.1. Clutch initiation, incubation periods, feeding visits, and fledging age for Amazona parrots

<table>
<thead>
<tr>
<th>Week (number of nests)</th>
<th>A. autumnalis (n = 24)</th>
<th>A. oratrix (n = 6)</th>
<th>A. viridigenalis (n = 26)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 = 19–24 March</td>
<td>3</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>2 = 25–31 March</td>
<td>4</td>
<td>3</td>
<td>7</td>
</tr>
<tr>
<td>3 = 1–7 April</td>
<td>10</td>
<td>1</td>
<td>10</td>
</tr>
<tr>
<td>4 = 8–14 April</td>
<td>5</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>5 = 15–21 April</td>
<td>1</td>
<td>0</td>
<td>5</td>
</tr>
<tr>
<td>6+ = after 22 April</td>
<td>1</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>&quot;Mean&quot; (week of initiation)b</td>
<td>3.00</td>
<td>2.33</td>
<td>3.23</td>
</tr>
<tr>
<td>Range (week of initiation)</td>
<td>1 to 6</td>
<td>1 to 4</td>
<td>1 to 6</td>
</tr>
<tr>
<td>Standard deviation</td>
<td>1.22</td>
<td>1.03</td>
<td>1.27</td>
</tr>
<tr>
<td>Coefficient of variation</td>
<td>0.41</td>
<td>0.44</td>
<td>0.39</td>
</tr>
<tr>
<td>Average initiation of clutch (date)c</td>
<td>2 April</td>
<td>31 March</td>
<td>5 April</td>
</tr>
<tr>
<td>Mean duration of incubation (days)</td>
<td>28d</td>
<td>28d</td>
<td>27 (n = 7)</td>
</tr>
<tr>
<td>Mean daily feeding visits to the nests</td>
<td>2.09</td>
<td>2.18</td>
<td>2.08</td>
</tr>
<tr>
<td>Range of daily visits to the nests</td>
<td>0–3</td>
<td>0–3</td>
<td>0–4</td>
</tr>
<tr>
<td>Mean age at fledging (days)</td>
<td>55 (n = 4)</td>
<td>57 (n = 2)</td>
<td>53 (n = 9)</td>
</tr>
</tbody>
</table>

aBased on nests inspected with a burrow probe in the 1993 and 1994 breeding seasons. For A. oratrix, two additional nests from the 1992 season were included to increase sample size; although no burrow probe was available in 1992, these two nests were shallow enough to be inspected directly.

bAn index calculated from six categories (weeks) assigned based on day of initiation. A test using Kruskal-Wallis on this index showed no difference among species (KW = 2.5, df = 2, p < 0.281).

cCalculated from actual date of initiation for each nest.

dAs reported in the popular captive breeding literature.

NEST SITE AND PAIR FIDELITY, AND CAVERY REUSE

In general, nest site and pair fidelity tend to be high for psittacine birds (Snyder et al. 1987; Rowley & Chapman 1991), although there are variations to be seen among species. High pair fidelity, for example, has been found in two species of Amazona in northeastern Mexico—the Red-crowned and Yellow-headed Parrots (Enkerlin-Hoeflich 1995), and as with nest fidelity, may often be associated with improved productivity as the years of experience accumulate. In many studies, cases of divorce have been largely limited to instances of reproductive incompetence of one of the pair members (Snyder et al. 1987; Rowley & Chapman 1991).
Maroon-fronted Parrots nest in colonies ranging from one or two to more than 100 pairs. Pairs seem to have strong site fidelity, at least to the same colony, if not the same nest hole, as demonstrated by returns of birds carrying radio transmitters over periods of several years. Similarly, established pairs of most *Amazona* exhibit a marked degree of philopatry. For example, in northeastern Mexico in 1993, four pairs of visually distinctive *Amazona* that switched nest sites moved to new nests within a 50 m radius of their previous nests. In 1994, five pairs had new nests within a 50 m radius of their previous nests and two pairs moved within a radius of only 100 m. The attachment to specific nesting areas can be something that occurs rapidly: a female Red-crowned Parrot released with a radio collar established her nest sites in two successive nesting periods in trees within 200 m of the release cage (Enkerlin-Hoeflich 1995).

At least six pairs of Red-crowned Parrots and five pairs of Yellow-headed Parrots individually recognizable by feather characteristics showed mate fidelity between successive nesting periods, and at least three of each species exhibited fidelity for three nesting periods. Such high mate fidelity has also been documented in the Puerto Rican Parrot by Snyder et al. (1987) and may be generally true in the genus *Amazona*. Fidelity to specific nest sites, however, is more variable. Enkerlin-Hoeflich’s (1995) studies of Red-crowned and Yellow-headed Parrots in 1993 and 1994 revealed that fidelity to specific sites was low compared to that reported in other *Amazona* (Snyder et al. 1987; Gnam 1991; Rojas-Suárez 1994). In large measure, this difference may reflect species differences in cavity availability, with suitable cavities being considerably more abundant for the Red-crowned and Yellow-headed Parrots than for other amazons, although additional factors may well have been involved as well. Nest switching is standard in many cavity-nesting birds (e.g., Boreal Owls, *Aegolius funereus*, and California Condors, *Gymnogyps californianus*—see Hayward & Hayward 1993 and Snyder & Schmitt 2002), and may offer general advantages, such as reductions in parasite infestations, that need to be balanced against advantages that may result from maintaining site fidelity, especially in cavity-poor environments.

In many species, there is a tendency for pairs to switch nest sites after failures to fledge young and a tendency to stay with nest sites after success in fledging young (Saunders 1982). One pair of Puerto Rican Parrots studied over many years followed this pattern religiously, while other pairs exhibited strong nest-site fidelity regardless of success or failure in the sites over the years (Snyder et al. 1987). As an aside, until it was learned that the latter pattern was the more typical one for this species, efforts to multiple-clutch wild pairs were held in abeyance because of concerns that such efforts would drive pairs into using new nest sites for replacement clutches that might be vulnerable to predation by Pearly-eyed Thrashers (*Margarops fuscatus*). But once the strong tendency of pairs to stick with nest sites, despite failure in the sites, was established, multiple-clutching efforts were initiated with considerable success and without causing pairs to abandon sites.

Even with relatively low levels of nest reutilization, pairs of Red-crowned and Yellow-headed Parrots have exhibited greater tendencies to reuse sites in which they have succeeded than sites in which they have failed. Similarly, studies of Maroon-fronted Parrot nesting colonies indicate that cavities producing fledglings are generally the cavities most frequently reused over several-year periods.

Thus there are reasons to suspect that poaching of entire broods from nests of many species may not only remove immediate reproduction but may also affect future reproduction by stimulating pairs to move to new and untested nest sites, both because poachers frequently destroy nest sites in harvesting them and because they often stimulate the birds to move even if they do not harm the nest sites. If instead parrot trappers were to allow at least one young to fledge per nest and were not to harm nest sites in harvesting young, both parrots and trappers might ultimately benefit from greater overall parrot populations and nest success in the populations. Instituting such relatively prudent harvesting procedures, unfortunately, is unlikely in areas subject to unregulated harvest, because maximization of short-term benefits tends strongly to overbalance maximization of long-term benefits.

**FEEDING BEHAVIOR AND RATES**

Amazon parrots of the mainland, such as Red-crowned Parrots of northeastern Mexico, almost