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THE COGNITIVE FACE OF AVIAN LIFE HISTORIES

The 2003 Margaret Morse Nice Lecture

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ABSTRACT.—Cognition includes the acquisition, processing, retention of, and acting upon information from the environment. Avian cognition has been investigated by the approaches of experimental psychology and in the context of specific tasks, such as spatial memory. However, the costs and benefits of cognitive ability have not been considered in a life-history context. I explore possible relationships between behaviors that might indicate cognitive function and other attributes, particularly brain size, rate of development, age at maturity, and life span. Large brain size and prolonged development are seen as potential costs of intelligent behavior. Long life span may permit the extended learning periods that support experienced-based cognitive function. Play behavior, which plausibly supports the development of motor and social skills, and, to a lesser extent, foraging innovations, are related to brain size. The challenge of foraging in a spatially and temporally varying environment, experienced for example by pelagic seabirds, is associated with prolonged embryonic development. Although these connections lack mechanistic foundations, they suggest that cognition can be considered as a part of the life history of the individual and that potential costs of cognition might provide guidelines for directing the comparative study of intelligent behavior. *Received 30 April 2004, accepted 7 June 2004.*

Over the course of her remarkable career, Margaret Morse Nice produced many original contributions to ornithology, including her pioneering studies on the life histories of birds (e.g., Nice 1937, 1943, 1957) and the development of behavior (Nice 1962). For many of us who were students during the 1960s, which was a period of transformation in ecology and behavior, her work laid the foundation for all that we set out to accomplish. It is this intersection of life history and behavior that I would like to address in this contribution. I am grateful to the Wilson Ornithological Society, and particularly to Jed Burtt, for giving me the opportunity (and a captive audience) for exploring ideas that have fascinated me for many years, but which have not come into clear focus until now.

Behavior provides the individual a flexible

relationship with its environment. The environment of every organism is varied in space and changes constantly through time, often unpredictably, but also with regularities that can be learned over time. Individuals respond to their environments in a variety of ways. Many behaviors are “hard-wired” into the nervous system and express evolved responses, available from birth, to consistent features of an individual’s surroundings. At the other extreme, organisms occasionally encounter novel situations for which they must devise novel solutions, what many of us would consider intelligent behavior. We suspect that species vary widely in terms of what we think of as intelligence; most ornithologists, if asked, would put parrots and corvids at the top of the avian intelligence scale and relegate doves and sparrows to lower positions, although one could argue that individuals of every species handle very well the tasks necessary for their survival and reproduction.

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I assume that most behavior is adaptive and contributes to the lifetime reproductive success, or fitness, of the individual. Variation in capacities for certain types of behavior presumably reflects different balances between the costs and benefits of such behavior in the context of demands of the environment. I also assume that the capacity to think is costly, at least in terms of the development and maintenance of the hardware required, and that if it is not necessary to think in a particular way, individuals should not bear the cost of that particular ability. This simple idea constitutes a life-history approach, which considers the conflicting contributions of adaptations to fitness resulting from the allocation of limited time, energy, tissue, and other resources. I find it remarkable that the evolution of intelligent behavior is rarely considered within a life-history framework. Indeed, one of the most widely respected textbooks in animal behavior that uses an evolutionary approach (Alcock 1998) does not list cognition in its index and under intelligence refers only to a single page devoted to the heritability of IQ.

In this essay, I have endeavored to treat thinking, or the capacity to think, in a life-history context. The fact that some birds appear to do less “thinking” than others suggests that thought might have substantial costs or that it might be highly constrained by other aspects of the life history. Of course, thought is hard to measure. It is possible, however, that some of the costs it incurs are not. These costs might involve maintaining a large brain and prolonging development to build a large, complex nervous system and acquire the experience necessary to perceive pattern in environmental variation. If this inference were correct, could we not use these presumed costs to indicate certain mental capacities? I shall use data on brain mass and the length of the incubation period for a large number of birds to construct a two-dimensional space representing some presumed costs of cognition. I will then determine whether certain kinds of behavior that are associated with cognitive ability (sociality, appearance of novel behaviors, play, experience-based foraging, for example) bear a relationship to presumed costs (some do!). Of course, patterns do not tell the whole story. However, we can use patterns to guide our thinking about thought in a

life-history context. Clearly, this is a crude beginning to a highly complex and difficult task. I hope, however, that this essay will encourage readers to regard intelligent behavior as integral to the life history of the individual and subject to selection that weighs its costs and benefits.

WHAT IS COGNITION?

According to Shettleworth (2001), cognition, broadly defined, “includes perception, learning, memory and decision making, in short all ways in which animals take in information about the world through the senses, process, retain and decide to act on it.” Vauclair (1996:10) sees cognition more narrowly as allowing an individual “to adapt to unpredictable changing conditions in its environment. Thus, behaviors that would aid adaptation would reflect several characteristics, such as *flexibility*, *novelty*, and *generalization*. Flexibility of behavior designates the possibility of constructing an adapted response to unusual external conditions. The response also must be novel in the sense that it does not express the existence of a pre-wired program. Finally, the novel behavior, established to solve a novel problem, must be susceptible to generalization to situations that differ partially or totally from those in which they were initially acquired.”

Many psychologists distinguish “between cognition, a possible means to an end, and intelligence, an assessment of performance judged by some functional criteria” (McFarland 1989:130). Intelligent behaviors are often regarded as specific adaptations to specific problems (Rozin 1976). For example, the sophisticated navigation abilities of pigeons appear to be highly intelligent (Wiltschko and Wiltschko 1993, 1998; Walcott 1996; Wallraff 2001), but because they are mostly controlled by hard-wired systems, these abilities cannot be generalized to other kinds of behavior. Thus, by Vauclair’s definition, they cannot be considered as an indication of general cognitive ability. It is entirely possible that intelligence and cognition defined in this manner represent points on a continuum and that the distinction, although perhaps heuristically useful, is artificial. Cognitive abilities themselves are certainly specialized in many respects. For example, Clark’s Nutcrackers (*Nucifraga col-*

umbiana) have a high degree of spatial cognition across many types of tasks, but perform less well with non-spatial information, such as color (Olson et al. 1995).

I shall adopt a broader definition of cognitive ability here to include the acquisition and processing of information from the environment as a basis for behavior. I hasten to add that the study of animal cognition is not the study of animal consciousness, although consciousness (self-awareness) should be considered as a type of cognitive behavior (Rozin 1976; Griffin 1984, 1985; Terrace 1984; Roitblatt 1987; Bekoff 2000).

Many researchers regard as central to cognition the concept of a cognitive map (Roitblatt 1982, 1987; Gallistel 1990; Gervet et al. 1996). Animals acquire and remember landmarks, attach values to them, and incorporate changes in these landmarks over time. Cognitive maps may represent physical space (Kamil and Jones 1997, Gibson and Kamil 2001), or they may relate to social “space,” predator “space,” weather “space,” and the like. A cognitive map is a representation of features of the world in the brain itself, and neurobiologists are beginning to discover the correspondence between the two (e.g., Jarvis and Mello 2000, Bingman and Able 2002).

HOW DO WE ASSESS COGNITIVE ABILITIES?

Corvids and parrots are generally regarded as intelligent and sociable (Takahashi and Keller 1994; Hunt 1996; Marler 1996; Cohen et al. 1998; Pepperberg 1999, 2002; Bugnyar et al. 2001; Balda and Kamil 2002; Bugnyar and Kotrschal 2002; Heinrich 2002; Hunt et al. 2002; Knudsen 2002). What does this mean? We have various tools for probing the cognitive abilities of animals. The most important of these comprise the methods of experimental psychology, in which mental capacities are assessed by performance in various kinds of behavior tests. A second approach, which may have broader application in comparative studies, is to record behavioral correlates of cognitive ability. Recently, the frequency of behavioral innovations has received attention in this regard (Lefebvre et al. 1997, 1998; Nicolakakis and Lefebvre 2000) and particular cases, such as tool making in New Caledonian Crows (*Corvus moneduloides*; Hunt 1996,

Chappell and Kacelnik 2002, Hunt and Gray 2002, Weir et al. 2002), have received considerable and well-deserved attention in the media. A third approach is to infer cognitive abilities from the kinds of problems that animals have to solve in their daily lives. That is, we can ask what kinds of mental function are needed for an individual to behave the way it does in its particular environment. For example, tracking nectar sources by hummingbirds (Garrison and Gass 1999, Bateson et al. 2003) and cache retrieval by jays (Balda et al. 1996; Griffiths et al. 1999; Clayton et al. 2001, 2003; Balda and Kamil 2002) may require more sophisticated spatial and temporal representations than leaf gleaning by warblers and ground foraging by doves.

Representation, which might be thought of as the formation of mental images, can be verified in its simplest form by various tests of memory (e.g., Griffiths et al. 1999, Clayton et al. 2001). Beyond this, experimental comparative psychology investigates problem-solving abilities associated with concepts of sets, identity and oddity, perceptual categories, serial learning, and imagery (Vauclair 1996). In an experimental setting, identifying the formation of sets, for example, involves a subject's ability to generalize the concept of similarity to novel objects; serial learning is revealed by the ability to construct a correct sequence out of a subset of sequentially presented stimuli; and so on. Many excellent reviews detail the results of experimental psychology (Pearce 1987; Gallistel 1989; Ristau 1991; Byrne 1994; Balda et al. 1996, 1998; Vauclair 1996; Shettleworth 1998; Griffiths et al. 1999; Pepperberg 1999; Heyes and Huber 2000; Clayton et al. 2001; Wynne 2001; Bekoff et al. 2002).

In a comparative, life-history framework, the approaches of experimental psychology become laborious and context dependent. For example, it is difficult to compare the results of psychological tests on species with varied communication modalities and different problem solving requirements in their lives. Therefore, the analyses in this discussion rely on various presumed behavioral correlates of cognitive function and inferences concerning cognitive function from the behavioral demands posed by tasks that organisms accomplish in their daily lives.

COGNITION AS A LIFE-HISTORY TRAIT

The benefits of cognition.—The value of cognition must involve functioning in a complex, variable environment where decisions conditioned by experience or reasoning are crucial. As explained by W. J. Smith (1990), cognitive function enables prediction and shapes expectation about the environment, including social interactions (see also Stephens 1989). Examples include food caching (Krebs et al. 1996, Gibson and Kamil 2001, Kamil and Cheng 2001), risk assessment associated with variable rewards (Real 1991, 1993; Kacelnik and Bateson 1996; Bateson and Kacelnik 1997; Garrison and Gass 1999; Marsh and Kacelnik 2002; Schlick-Paim and Kacelnik 2002), context-dependent responses to social signaling (W. J. Smith 1990), social negotiation based on shared information (Smith 1997, 1998), and reciprocal altruism depending on long-term association with identifiable individuals (Trivers 1971, Axelrod and Hamilton 1981).

The costs of cognitive ability.—The association of well-developed cognitive abilities with a large brain may be a particularly human conceit, but many studies of differences in behavior among species are generally consistent with such a relationship (Jerison 1973, Clutton-Brock and Harvey 1980, Macphail 1982, Dunbar 1992) and certain measured cognitive abilities are related to the size of relevant parts of the brain. I am referring in particular to the relationship between spatial memory and the size of the hippocampus (Healy and Krebs 1996, Biegler et al. 2001), but similar structure-function connections are evident with respect to other behaviors, such as singing, and related brain regions (Brenowitz et al. 1985, Brenowitz and Arnold 1986, Devoogd et al. 1993, Bernard et al. 1996), although one must exercise caution in generalizing such connections (Aboitiz 1996, 2001).

The brain is thought to be an expensive organ metabolically (Field et al. 1939, Martin and Fuhrman 1955, Aiello and Wheeler 1995) and large brain size presumably also applies architectural stresses on morphology and aspects of animal function (Aboitiz 1996). Flight itself may impose some limits on brain size. Another cost of a larger brain or more precise and complex neural connections with-

in the brain may be prolonged development. The basic architecture of the brain and most of its growth occurs before birth in mammals (Pagel and Harvey 1988), and this is also true in birds (Portmann and Stingelin 1961; Starck 1993, 1998; Ricklefs and Starck 1998). Birds exhibit tremendous variation in the length of the incubation period—more than a factor of three when incubation period is normalized by egg size (Ricklefs 1993). Costs of prolonged incubation include increased exposure to time-dependent mortality, higher energy requirements of embryonic growth, and increased reproductive stress for parents. The benefits of long incubation periods have not been identified, although presumably they reflect a higher quality chick (Ricklefs 1992, 1993).

A more cognitive life style might also be associated with a long learning period to acquire information, leading to delayed reproduction and reduced lifetime reproductive success. For example, increased cognitive ability might carry with it the opportunity to exploit a type of food supply that is not available, or is less efficiently used, without acquiring extensive information about temporal and spatial distribution of prey or of suitable foraging conditions. Complex social settings may require learning appropriate responses to individual variations in behavior and signaling.

CAN WE RECOGNIZE COGNITIVE ABILITIES BY THEIR ASSOCIATED COSTS?

I believe that the most obvious candidates for costs are brain size and embryonic development period. Postnatal growth rate and age at maturity are also reasonable choices in that they reflect a substantial portion of brain growth and development and the most significant part of an individual's learning period. In fact, these measures are generally correlated with embryonic development.

The relationship between brain mass and body mass in birds is shown in Figure 1. The residuals from the logarithmic regression provide a body mass-specific index to relative brain size. Averaged over larger taxonomic groups of birds (Sibley and Monroe 1990), these residuals identify several families with larger-than-average brain mass: Psittacidae, Strigidae, Corvidae, Picidae, Bucerotidae. It is not surprising to find the parrots and corvids

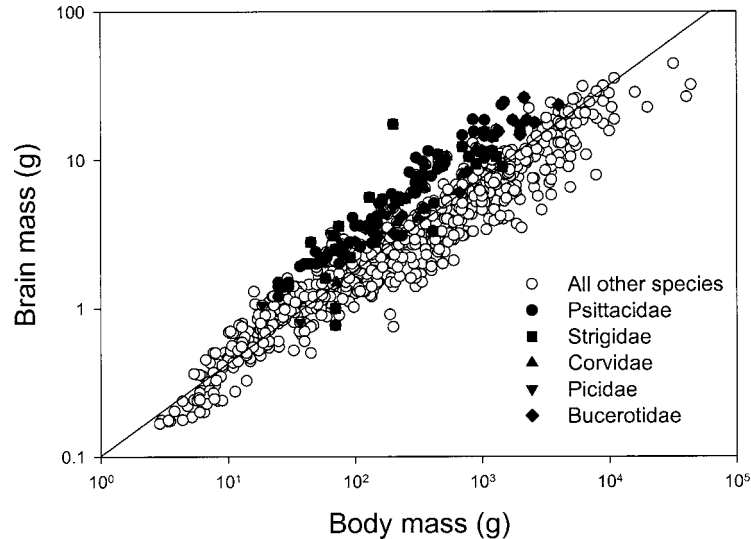


FIG. 1. Relationship between brain mass and body mass in birds based on data for 837 species in 104 families (for details, see Nealen and Ricklefs 2001). Regression within orders ($n = 23$) $F_{1,780} = 6590$, $P < 0.001$, slope = 0.625 ± 0.008 , intercept = -0.997 ; thus, the equation is $\log \text{brain} = -0.997 + 0.625 \times \log \text{body}$. $R^2 = 0.952$, RMSE (within orders) = 0.114. Order effect: $F_{22,780} = 48.8$, $P < 0.001$. Residuals are calculated from this regression line. Among families represented by more than 10 individuals, those with the highest residual brain masses were Psittacidae (0.27 ± 0.10 SD, $n = 49$), Strigidae (0.25 ± 0.17 , $n = 24$), Corvidae (0.24 ± 0.10 , $n = 21$), Picidae (0.22 ± 0.11 , $n = 13$), and Bucerotidae (0.15 ± 0.07 , $n = 13$). Those with the lowest residuals were Phasianidae (-0.30 ± 0.11 , $n = 39$), Columbidae (-0.22 ± 0.10 , $n = 21$), Anatidae (-0.14 ± 0.09 , $n = 64$), Scolopacidae (-0.12 ± 0.05 , $n = 27$), and Trochilidae (-0.12 ± 0.06 , $n = 27$).

near the top of the list, and hornbills are also known for complex social behavior (Kemp 1995), which might be indicative of well-developed cognitive abilities. Owls have very sophisticated foraging methods involving complex processing of auditory information (Takahashi and Keller 1994, Cohen et al. 1998, Knudsen 2002). I must have underestimated woodpeckers in the past, although Acorn Woodpeckers (*Melanerpes formicivorus*) certainly exhibit complex social behavior (e.g., Koenig and Mumme 1987, Koenig et al. 1998). Families on the bottom of the list of relative brain size are Phasianidae, Columbidae, Anatidae, Scolopacidae, and Trochilidae. It is notable that three of these groups have precocial offspring whose brains are well developed at hatching (Ricklefs and Starck 1998). It may also be significant that four of these groups constitute the bulk of bird species that have been hunted commercially and for sport.

The relationship between incubation period and egg mass in birds is shown in Figure 2. Again, residuals from the logarithmic regres-

sion provide an index to relative incubation period. In this case, taxa with exceptionally long incubation periods include Procellariiformes, Accipitridae, Spheniscidae, Psittacidae, Strigidae, Bucerotidae, and Falconidae. Three of these families also have exceptionally large relative brain size. In addition, the group includes two lineages of seabirds and most raptorial birds. On the low end of the scale are the Picidae, Columbidae, Fringillidae, Muscicapidae, and Passeridae, all of which have extremely altricial development and tend to have small body sizes.

Residuals from the brain mass and incubation period regressions define a space within which any particular group of birds can be placed. Within this space, the presumed cost of cognition increases with larger relative brain size and longer relative embryonic development, and this is where one expects to find birds with the most developed cognitive abilities. Because we have little direct comparative information on the cognitive capacities of birds, with the exception of pigeons, parrots, and corvids, I shall consider several

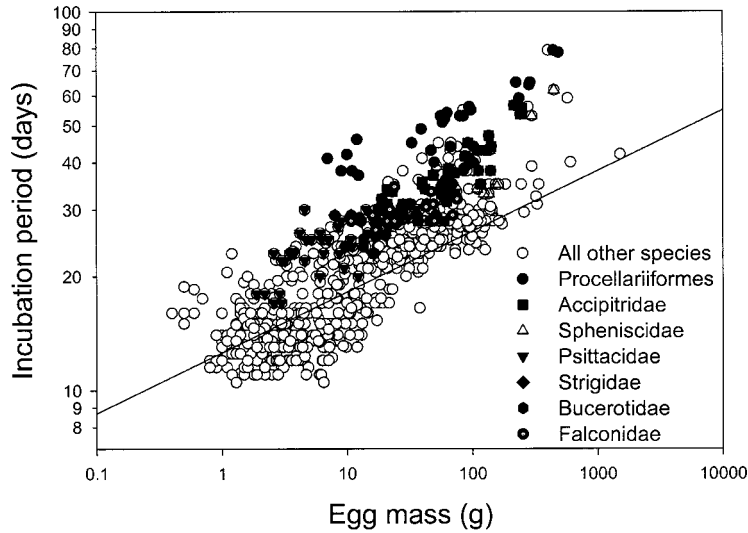


FIG. 2. Relationship between incubation period and egg mass in birds based on 799 species in 19 orders (for details, see Ricklefs 1993). Regression within orders ($n = 19$) $F_{1,776} = 203$, $P < 0.001$, slope = 0.160 ± 0.008 , intercept = 1.099 ± 0.073 ; thus, the equation is $\log \text{incubation period} = 1.099 + 0.160 \times \log \text{egg mass}$, $R^2 = 0.833$, RMSE (within orders) = 0.073. Order effect: $F_{18,776} = 35.1$, $P < 0.001$. Residuals are calculated from this regression line. Among taxa with exceptionally long relative incubation periods are Procellariiformes (0.323), Sulidae (0.239), Accipitridae (0.174), Trochilidae (0.172), Apodidae (0.156), Spheniscidae (0.153), Psittacidae (0.146), Strigidae (0.137), Bucerotidae (0.135), and Falconidae (0.135). Those with exceptionally short incubation periods include Sturnidae (-0.119), Picidae (-0.088), Columbidae (-0.067), Fringillidae (-0.053), Muscicapidae (-0.048), and Passeridae (-0.031).

behavior indices that might plausibly be related to cognition: (1) cooperative breeding; (2) sociality, or group living; (3) play behavior; (4) foraging innovations; and (5) challenging foraging situations. I shall also compare the putative costs to life span (which is also closely related to age at maturity) to assess the idea that some types of cognitive behavior require extensive learning periods.

Cooperative breeding.—My criterion for cooperative breeding for each family or other large taxonomic group is the proportion of species exhibiting helping behavior, reported by Jerram Brown (1987:table 3.1). The rationale for using cooperative breeding as an index to cognition is that in many family or extended family groups, individuals discriminate the recipients of helping behavior on the basis of relationship, which requires the learning of kin relationships (Emlen et al. 1995). The taxonomic groups with the highest proportion of helping, according to Brown's summary, are the hornbills, other coraciiforms, grebes, corvids, and mousebirds. Hornbills and corvids also get high scores for the putative costs of

cognition. In general, however, the proportion of species with helping behavior is unrelated to either relative brain mass or relative incubation period. In a stepwise multiple regression of the proportion helping (SAS PROC GLM), neither relative brain mass ($F_{1,20} = 0.46$, $P = 0.50$) nor relative incubation period ($F_{1,20} = 2.96$, $P = 0.10$) were significant effects (total $R^2 = 0.142$). In retrospect, helping behavior is probably not a good cognition index because, in essence, helping merely combines failure to disperse with what all birds with altricial development do naturally, that is, feed offspring.

A more pertinent index might be the capacity to develop complex interactions within and among extended family groups in species with social breeding, where reproductive success may hinge on personal knowledge of, and long-term association with, other individuals in the group. For example, among the species of cooperatively breeding birds detailed in Stacey and Koenig (1990), those engaging in colonial breeding belonged to coraciiforms

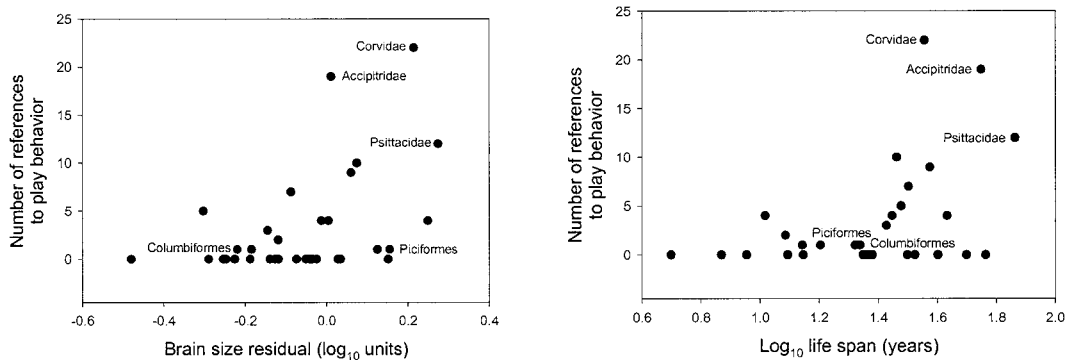


FIG. 3. Relationship between number of publications describing play behavior and relative brain size (left) and life span (right). From data compiled by Fagen (1981).

and corvids (J. N. M. Smith 1990:table 2), taxa with relatively large brains.

Sociality.—Group living balances benefits of group defense and social foraging against the costs of local competition for resources and social strife. Social behavior is thought by many authors to go hand in hand with cognitive behavior and brain size in primates (Sawaguchi 1990, 1992; Dunbar 1992, 1993). The “social complexity hypothesis” states that living in large groups selects for enhanced cognitive abilities with respect to recognizing individuals and assessing social relationships (Cheney and Seyfarth 1990, Byrne and Whiten 1997, Kummer et al. 1997). Support for this hypothesis has recently come from experimental studies on cognitive abilities in jays (Bond et al. 2003). My criterion for group living was the tendency to form groups with complex social structure. Both parrots and corvids place high on the list of such taxa, but to keep things simple I subjectively assigned taxa a score of either 0 or 1. Among the less social taxa are ducks, doves, cuckoos, quail, oscine passerines, and raptors; among the more social taxa are parrots, corvids, many seabirds, and many coraciiforms. Again, as in the case of helping behavior, group living was not a significant effect in an analysis of variance (ANOVA: SAS PROC GLM) for either relative brain mass ($F_{1,33} = 2.04$, $P = 0.16$, $R^2 = 0.058$) or relative incubation period ($F_{1,30} = 0.95$, $P = 0.34$, $R^2 = 0.031$). Nor did a discriminant analysis with body size, relative brain mass, and relative incubation period distinguish social versus non-social species ($F_{3,28} = 0.69$, $P = 0.57$). Different observers would

assign different scores, but the result probably would not change. Again, the problem with group living as an index to cognition is that many associated behaviors may require little more cognitive capacity than the kinds of cooperative and antagonistic interactions that all birds engage in, whether social or not. A better understanding of more complex behavior in social species based on individual knowledge and association might lead to a better index (e.g., W. J. Smith 1990, 1998), but this is beyond my understanding of bird societies.

Play.—Play is a more promising indicator of cognitive abilities because play presumably represents practice behaviors that refine physical and social skills (Fagen 1981, Byers and Walker 1995, Bekoff and Byers 1998). Unfortunately, there is no widely accepted definition of play in birds and comparative studies of avian play behavior are largely lacking. We all know play when we see it, but many reports of play in the ornithological literature are similarly anecdotal. I have taken as my index to play the number of publications describing play behaviors listed in Tables 3–26 to 3–28 of Fagen (1981). The taxa that come out on top of this list are falcons, passerids, parrots, accipiters, and corvids. The sample is undoubtedly biased by the large number of studies on these groups; however, it is noteworthy that each of these five taxa has above-average relative brain size (Fig. 3). The data were analyzed by a stepwise multiple regression, with body mass, relative brain mass (rbrain), relative incubation period, and life span as independent variables. In this analysis, brain size ($F_{1,26} = 7.0$, $P = 0.014$) and life

span ($F_{1,26} = 5.85$, $P = 0.023$) explained 37% of the variance in number of citations of play behavior. Relative brain size by itself explained 23% of the variance ($F_{1,27} = 8.1$, $P = 0.008$, play = $4.42 [\pm 1.00] + 17.29 [\pm 6.08]$ rbrain).

Foraging innovations.—Louis Lefebvre and his colleagues at McGill University have recently tabulated reports of foraging innovations from the literature. Lefebvre et al. (1997) define foraging innovation as “either the ingestion of a new food type or the use of a new foraging technique,” generally a behavior reported either for the first time or as being highly unusual for a given species. These include such diverse behaviors as an American Kestrel (*Falco sparverius*) drowning a Red-winged Blackbird (*Agelaius phoeniceus*), a Hooded Merganser (*Lophodytes cucullatus*) depredating an adult meadow vole (*Microtus pennsylvanicus*), and sparrows searching car radiator grills for insects. Here, I use as an index the proportion of papers on a particular taxonomic group that describe foraging innovations, compiled for North American and Australian birds by Lefebvre et al. (2001). Thus, this index is corrected for research effort. Incidentally, more than half of the reported innovations in North American birds come from the pages of *The Wilson Bulletin*, which remains one of the few ornithological journals that publishes natural history observations.

Lefebvre and his colleagues have shown that the incidence of foraging innovations is positively related to brain size (Lefebvre et al. 1997, 1998, 2001). My analysis also reveals such a relationship, although it is weak ($r = 0.38$, $P < 0.05$; arcsin-transformed: $r = 0.46$, $P = 0.016$, $n = 27$). The taxa with the highest incidence of reported foraging innovations were the cranes and their relatives (Gruidae), falcons (Falconidae), parrots (Psittacidae), hummingbirds (Trochilidae), rails and their relatives (Rallidae), and swifts (Apodidae). Multiple regression showed that incidence of foraging innovations is unrelated to body mass, relative incubation period, mode of development, and life span. How foraging innovation might be related to inherent acceptance or avoidance of new stimuli (neophobia) is an interesting, but unexplored problem (e.g., Marples et al. 1998, Greenberg and

Mettke-Hofmann 2001, Mettke-Hofmann et al. 2002).

The challenge of finding food.—Feeding is a behavior common to all birds, however, different prey present widely different behavioral challenges. I presume that the most challenging types of prey resources are those that exhibit extreme temporal and spatial heterogeneity, such as the prey of most pelagic seabirds, or those that have well-developed abilities to sense and evade predators, such as the prey of many raptorial birds (see also, Clutton-Brock and Harvey 1980, Milton 1988, Dunbar 1992). Other birds handle special challenges, such as those which feed by traplining on changing arrays of flowers (hummingbirds) or widely dispersed fruiting trees (some tropical frugivores). I regarded species that feed on fine-grained food resources, where success is proportional primarily to searching time rather than special searching strategies (foliage gleaners, most seed-eaters, for example), as not requiring well-developed cognitive abilities. I classified foraging as very challenging (2: raptors, swifts, seabirds), moderately challenging (1: corvids, parrots, hummingbirds, plovers, flycatchers, woodpeckers, several tropical fruit-eating groups), and less challenging (0: most opportunistic ground feeders, waterfowl, most passerines).

Analyses of variance with foraging challenge as the main effect were not significant for body mass ($F_{2,32} = 2.82$, $P = 0.075$), but were highly significant for relative brain size ($F_{2,32} = 8.27$, $P = 0.001$, $R^2 = 0.34$) and relative incubation period ($F_{2,29} = 7.06$, $P = 0.003$, $R^2 = 0.33$) (Fig. 4). Relative incubation period increased from foraging class 0 (0.017 ± 0.072 SD, $n = 17$) to class 1 (0.073 ± 0.084 , $n = 11$) and class 2 (0.149 ± 0.071 , $n = 7$); relative brain size increased from foraging class 0 (-0.153 ± 0.141 , $n = 17$) to class 1 (0.062 ± 0.129 , $n = 11$), but was not significantly higher in class 2 (-0.023 ± 0.152 , $n = 7$). Because mode of development is associated with both brain size (precocials smaller) and incubation period (precocials longer), I analyzed the data again only for taxa with altricial development. Precocial species, except plovers, which actively pursue mobile prey, were placed in challenge class 0. In this second analysis without precocial species, relative brain size was no longer significant ($F_{2,18}$

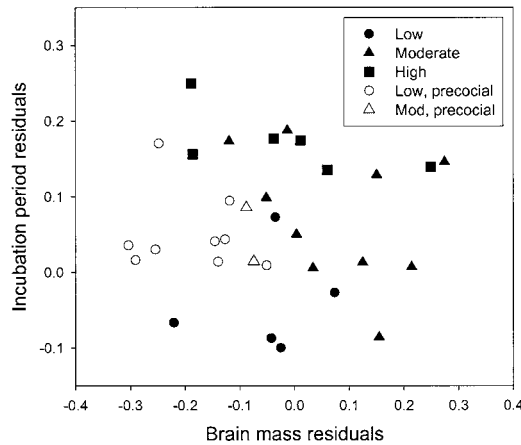


FIG. 4. Groups of birds exhibiting different levels of foraging challenge (circles: low, triangles: moderate, squares: high) as a function of relative brain mass and relative incubation period. Groups with altricial development are shown as filled symbols, those with precocial development as open symbols.

= 1.96, $P = 0.17$), body size was marginally significant ($F_{2,18} = 3.7$, $P = 0.046$, $R^2 = 0.30$), and relative incubation period explained a larger proportion of the variance ($F_{2,18} = 12.7$, $P < 0.001$, $R^2 = 0.60$). Mean relative incubation periods for the foraging classes were (class 0: -0.042 ± 0.070 SD, $n = 5$; class 1: 0.059 ± 0.084 , $n = 9$; class 2: 0.172 ± 0.042 , $n = 6$).

DEMOGRAPHY AND COGNITION

Long life span is strongly associated with a low reproductive rate, delayed maturity, and slow rate of senescence (Ricklefs 1973, 2000; Ricklefs and Scheuerlein 2001). Long life span may also promote the ability of an individual to make use of well-developed cognitive capacities owing to long learning periods, including apprenticeships with older individuals, and extensive experience with temporal and spatial variation in the environment. Most species present evidence of improved reproductive success with experience and age (Coulson 1966, Ollason and Dunnet 1978, Newton 1985, Perrins and McCleery 1985), which may be attributed to the acquisition of information rather than the development of physical skills. Thus, it is reasonable to ask whether species with long life spans demonstrate higher cognitive skills or costs associated with cognition.

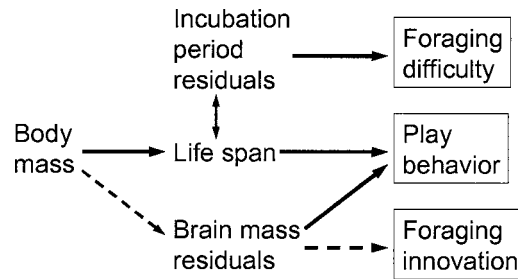


FIG. 5. Connections between life-history variables and indicators of cognitive function revealed by analyses in this study. Dashed arrows indicate weak correlations.

I used as a measure of life span the maximum longevity for a taxonomic group reported in the compilation of Carey and Judge (2000). Among the taxa sampled in this analysis, life span is positively correlated with body mass ($r = 0.43$, $P = 0.017$, $n = 30$), relative incubation period ($r = 0.48$, $P = 0.009$, $n = 29$), and number of publications reporting play behavior ($r = 0.65$, $P = 0.006$, $n = 16$), but not relative brain mass ($r = 0.25$, $P = 0.19$, $n = 30$). Neither the proportion of species exhibiting cooperative breeding ($r = -0.251$, $P = 0.27$, $n = 21$) nor the frequency of reports of innovation ($r = 0.24$, $P = 0.23$, $n = 26$) was significantly related to life span. Life span also did not differ among taxa in different foraging challenge classes ($F_{2,27} = 0.85$, $P = 0.44$). Taxa with higher tendencies to form social groups had marginally longer life spans than less social taxa ($F_{1,28} = 4.5$, $P = 0.042$, $r^2 = 0.14$).

Connections between behavior and life-history variables found in this analysis are diagrammed in Figure 5. Play behavior and foraging innovations are positively related to large brain mass and, in the case of play, long life. Challenges of foraging are more closely associated with relatively long incubation period, which itself is correlated with life span. Thus, several life-history traits might be associated with well-developed cognitive abilities: large brain size, complex brain structure, and slow development as costs (or enabling adaptations); high parental investment, delayed maturity, and long life span as associated traits; and complex foraging and social behaviors as benefits.

DIFFERENT WAYS OF BEING INTELLIGENT

The association of challenging foraging with embryonic development and the association of play and foraging innovation with brain size raises the question of whether there are different ways of being intelligent, each of these relationships representing different components of cognitive ability. Many authors have made the distinction between special and general intelligence, the difference essentially between experience-based decision-making and reasoning (Rozin 1976, McFarland 1989, Vauclair 1996). The first might be thought of as being retrospective, building on the accumulation of information about the environment and processing it in ways to make predictions based on past experience. The ability of seabirds to find their way over thousands of kilometers of ocean and locate quality foraging areas (Jouventin and Weimerskirch 1990, Prince et al. 1992, Weimerskirch and Wilson 2000) may require the accumulation of experience with correlations between weather, oceanographic conditions, and foraging success. If this were true, waiting up to 10 years to achieve sexual maturity (see Ricklefs 1973, 2000) might represent a learning period necessary before an individual can feed even a single chick successfully. Why such a capacity for learning might be related to the length of the embryonic development period rather than brain size is unclear. If this type of information accumulation and processing required an unusually large number of connections per neuron rather than a large number of neurons, the time element might represent the difficulty of making so many connections.

The second kind of cognition might be thought of as prospective, the ability to work out a novel solution to a novel problem, perhaps involving the generation of predictive scenarios based on accumulated experience and detailed observation. However, why this kind of thinking might require a large brain rather than a complex brain is unclear. Nonetheless, the analyses presented here indicate that those birds with relatively higher capacities for reasoning and problem solving, such as corvids and parrots, tend to have large brains.

Do certain preconditions facilitate the evolution of enhanced cognitive abilities?—If certain types of thinking are associated with such life-history traits as large body size, long life span, and prolonged development, the evolution of these traits for other reasons might facilitate the evolution of cognitive ability. Distinguishing preconditions from correlated evolution of traits requires analysis of the distribution of traits on a well-supported phylogenetic hypothesis. Information concerning this issue might also be obtained from the lability of traits within a phylogeny. Conservative traits are more likely to have preceded the evolution of more labile traits owing to their longer histories. However, disparity in the lability of traits also would signal an uncoupling of their evolution. Both relative incubation period and relative brain size are conservative, with most of their variance occurring on the level of families within orders or even higher (Fig. 6). Because we do not have adequate measures of cognitive abilities, it is difficult to determine whether these have a comparable distribution of variance or are more labile. Where groups of birds have been looked at closely with regard to behavior, researchers have tended to emphasize differences between closely related species rather than their similarities or, alternatively, the differences between larger taxonomic groups (Devoogd et al. 1993, Healy and Krebs 1996, Balda et al. 1997, Balda and Kamil 2002). Perhaps differences between closely related species represent the evolutionary elaboration of more generally shared abilities where species are challenged to perform disparate specific tasks.

Consideration of the evolution of cognition leads to another question, namely whether variation in cognition is graded or exhibits thresholds across which abilities change rapidly. This question frequently arises in discussions about the evolution of human intelligence. Some authors suggest that at some point in our evolutionary lineage brain size and intelligent behavior became self-accelerating and our cognitive abilities increased rapidly, creating a substantial gap between humans and other primates in both brain size and intelligent behavior (e.g., Dunbar 1993, Abou-tiz and Garcia 1997). Similar thresholds at lower levels of cognitive ability might also lead to the creation of gaps in intelligent be-

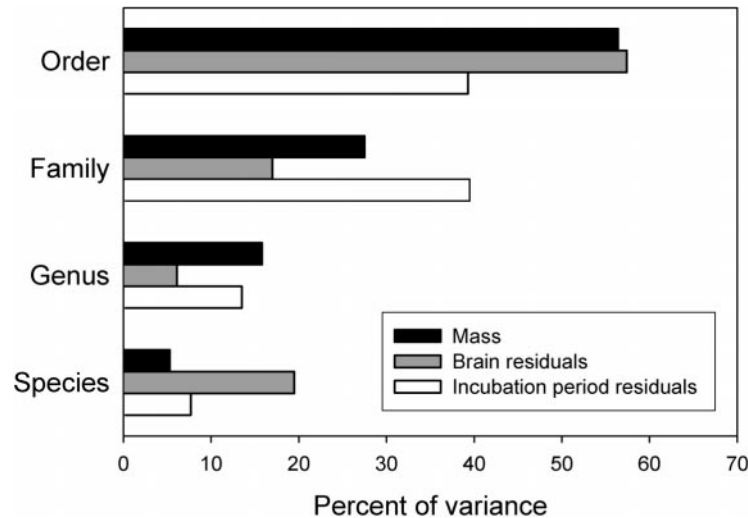


FIG. 6. Distribution of variance components among taxonomic levels for body mass, relative brain size, and incubation period. The relatively high residual for relative brain mass at the species level probably represents, in part, measurement error (i.e., the difficulty of measuring brain mass accurately and the lack of consistency of measurement techniques between studies). For details concerning data and sources, see Ricklefs (1993) and Nealen and Ricklefs (2001).

havior between some species and their close relatives. If the evolution of cognition were similar in different lineages, this might result in well-marked categories of cognitive function across birds, with different lineages having crossed one or more cognitive thresholds. Of course, available data illuminate this issue inadequately, and little more can be said about it at this point, except to remind ourselves how little we know about the evolution of cognition as a life-history trait.

CONCLUSIONS

The ability to act on accumulated experience and the ability to apply reasoning to novel situations are well expressed among birds, although species also differ widely in these abilities. Cognition can be treated as one or, more likely, a set of life-history traits having fitness benefits and costs to the individual. Therefore, it might be possible to judge aspects of cognitive ability indirectly by their associated costs, which plausibly include relative brain size and relative development time. As we understand intelligent behavior better and can place such behavior in a broadly comparative framework, we might develop a more refined definition of the costs of cognition and

improve our ability to recognize cognitive function.

Variation in both relative brain size and relative incubation period resides at a high taxonomic level, suggesting evolutionary conservatism. If these life-history traits are associated with cognition, as argued here, then it is plausible that the evolution of intelligent behavior is also conservative, requiring substantial evolutionary change in structure and development. This contradicts, to some degree, well-documented contrasts between cognitive abilities of some closely related species in particular tests, especially those concerning spatial memory. These different viewpoints might be reconciled if the capacity for intelligent behavior were conservative, but its realization were more labile.

The strongest correlations between putative costs of cognition and intelligent behavior identified in this analysis were associated with play behavior (brain mass) and the challenge of foraging (incubation period). Although the meaning of these statistically significant relationships is obscure, they suggest ways of developing a more broadly comparative appreciation of differences in the behavioral relationships of species to their environments. The

future of this effort to understand cognitive ability as a life-history trait depends on the development of comparative field and experimental studies on many aspects of behavior in birds, combined with a broad assessment of nervous system structure and development.

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