

Life History and Social Learning: Megapode Chicks Fail to Acquire Feeding Preferences From Conspecifics

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Australian brush-turkeys, *Alectura lathami*, are birds with an unusual life history: The young receive no parental care and first encounter conspecifics at an unpredictable age. Brush-turkey chicks that were 3–4 days old were presented with a robot model that appeared to feed from a distinctively colored dish. In control training trials, chicks saw a robot standing next to a different dish and scanning from side to side. Chicks expressed a strong tendency to feed from dishes of the type indicated by the pecking robot, but this effect proved ephemeral. Brush-turkeys hence appear to show no social learning under conditions that inculcate stable preferences in other galliforms such as chickens, suggesting that life history plays an important role in the evolution of learning.

Animals can acquire new patterns of behavior and increase the efficiency of decision making by observing or interacting with companions. Such social learning often provides functional benefits (see reviews in Galef & Giraldeau, 2001; Heyes & Galef, 1996; and Shettleworth, 1998; but see Giraldeau, Valone, & Templeton, 2002). The acquisition of food preferences has received particular attention in the study of social learning: By watching others feed, individuals learn to accept novel items and to identify toxic or noxious ones (reviews in Galef & Giraldeau, 2001; Lefebvre & Bouchard, 2003; Sherwin, Heyes, & Nicol, 2002). Young animals, in particular, benefit from such experiences. They can develop a preference for the same food as their parents while feeding with them, either through passive observation (Hikama, Hasegawa, & Matuzawa, 1990) or because adults enhance the rate at which offspring learn about food by performing specific behaviors (Galef & Allen, 1995; Nicol & Pope, 1996).

Burmese jungle fowl, *Gallus gallus spadiceus*, and their domesticated relative, *Gallus g. domesticus*, have been the subjects of much previous work on the social transmission of feeding behavior. Pullets change their food preferences after observing conspecifics feed; both adults (Nicol & Pope, 1996) and similar-age chicks are effective models (Johnston, Burne, & Rose, 1998; McQuoid & Galef, 1992). Young chickens also change their

pecking preferences in response to model hens (Turner, 1965), model beaks that “peck” (Suboski & Bartashunas, 1984), and video-recorded sequences of adults (McQuoid & Galef, 1993).

In the present study, we tested for social learning in chicks of the Australian brush-turkey, *Alectura lathami* (galliformes), a megapode species related to the domestic fowl but with a completely different life history. Brush-turkey chicks receive no parental care and live independently from the moment they hatch (Göth, 2001, 2002; Göth & Proctor, 2002; Jones, Dekker, & Roselaar, 1995). They never form bonds with adults, but do occasionally aggregate in small groups with other similar-age chicks, both in the wild (Göth & Vogel, 2002b) and in captivity (Göth & Jones, 2003). However, the timing of such social experience is unpredictable because chicks hatch asynchronously, disperse widely, and live in dense vegetation (Göth & Vogel, 2003). As a result, most chicks spend their first weeks on their own.

In summary, whereas young fowl predictably feed gregariously with their parents and hence can acquire socially transmitted preferences, young brush-turkeys must search for food alone and cannot depend on social cues. By comparing our results with the well-established pattern in fowl, we hoped to obtain insights into the evolutionary interaction between social systems, life histories, and the probability of learning (Lefebvre & Giraldeau, 1996; Shettleworth, 1998, pp. 473).

Experimental techniques were based on previous work in which we investigated the cues responsible for social aggregation in brush-turkeys. Naturalistic robot models of hatchlings proved to be highly effective stimuli, evoking approach and foraging behavior (Göth & Evans, 2004). In the present study, we used robots to manipulate social experience while retaining precise control over the behavior of a simulated companion. Design and test procedures were based on published work with fowl to facilitate comparison (McQuoid & Galef, 1992). Hatchling brush-turkeys were exposed to a pecking robot apparently feeding from a distinctively marked dish. Control training sessions of the same duration provided experience with a robot engaged in side-to-side scanning movements, next to a different dish. In subsequent test sessions, chicks were given a choice between the two types of dish to determine

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whether simulated feeding behavior had inculcated a specific socially transmitted preference.

Method

Chicks: Origin and Raising Conditions

Brush-turkeys incubate their eggs using the heat produced by microbial decomposition of organic material in mounds of leaf litter. Eggs were collected from natural incubation mounds in the Central Coast region north of Sydney, New South Wales, Australia and then were incubated artificially (Brinsea Octagon 250 Incubators) in conditions that match those in nature (temperature, 31–36 °C; humidity, 80–95%).

After hatching, chicks were held individually in boxes that visually isolated them from other chicks. These were equipped with a 40W red heat lamp and a branch for roosting, and were fitted with an artificial grass mat across which the chicks could move comfortably. It was not necessary to provide food and water during this period because brush-turkey hatchlings normally depend on their internal yolk reserves while digging themselves out of the soil after hatching, a process that requires an average of 40 hr (Göth, 2002).

On their second day of life, chicks were transferred to individual outdoor pens (3 m × 3 m and 3 m high) located in an undisturbed forest (Macquarie University Fauna Park). Each pen provided roosts and shelter and was visually isolated from adjacent pens by opaque fabric on the side walls. Chicks were fed protein-rich crumble food and water *ad libitum*, with vitamin supplements. The floor of the aviary was covered with mulch, which enabled the chicks to forage for invertebrates as they would naturally. No attempt was made to food-deprive chicks prior to experiments. The circular division fence used in subsequent experiments (see below) was placed in the aviary before the chicks were introduced so that they could become familiar with it. After testing, chicks were kept in groups of up to 7 until release at the place of origin, at the age of 1–3 weeks.

Stimuli

Experiments involved the presentation of robot models of conspecific chicks and of differently colored dishes containing corn. We adopted this approach to simulating the presence of a social companion because it allowed us to control stimulus properties while preserving realism. In particular, we wished to avoid complex interactions of the sort that would inevitably occur between a live demonstrator and subjects.

We constructed three “pecking robots” and one “scanning robot” from taxidermically prepared mounts of 3-day-old chicks that had died naturally. These contained an electric servo motor (“Nagro,” Grand Wing Servo-tech, Hsichih, Taipei, Japan) operated by radio control (“Attack” two-channel system, Futaba Bioengineering, Irvine, California, U.S.A.). The motor moved the chick body in either a vertical plane (pecking movement) or a horizontal one (scanning movement) while the feet remained stationary (see Figure 2 in Göth & Evans, 2004). During pecking, the head moved from a static position (in which the beak was pointing forward) downward, until it made contact with the corn in a dish. During scanning, the robot performed horizontal movements of the whole body, through an angle of 45° to both sides of the resting position. Robots were moved in bouts of 10 pecking or scanning movements, with a total duration of 6.5–8 s. We varied the intervals between movement bouts from 1–4 min to reduce habituation.

The food dishes used in training and subsequent test trials were square (6 cm × 6 cm) and made of transparent plastic. To make them visually distinctive, we added nine red or blue adhesive labels (1.3 cm diameter) evenly spaced 5 mm below the rim; we refer to these as the “red dish” and the “blue dish” for brevity. A previous study had shown that chicks have no spontaneous preference for one of these colors over the other, despite their well-developed color vision (Göth & Proctor, 2002).

Design and Test Procedure

Experiments started on the third or fourth day of life, in the chicks’ home pens. The experiments consisted of a training session on the first and second day, followed by a test session on the third day, each lasting for 20 min.

During training sessions, a pecking or scanning robot was positioned in front of either a blue or red dish, and a dish of the other color was presented 30 cm away (see Figure 1). A second pair of red and blue dishes was placed opposite these, to provide alternative choices for chicks too fearful to approach the robot closely. The dishes contained corn, which brush-turkey chicks prefer over other types of fruit and vegetables with which they are familiar (Ann Göth, personal observation). All four dishes and the robot were encircled by a 25-cm high division fence made of green chicken wire, which prevented the chicks from accessing the food in the dishes (see Figure 1). Brush-turkey chicks usually walk rather than fly, and no chick ever flew into the arena.

We chose not to allow the chicks to feed on the corn during training trials because previous studies have shown that birds can use both individual experience and observation of others in a foraging context; our goal was to test for the formation of preferences based on social cues alone. It is well established that birds can respond differentially to stimuli indicated by a demonstrator without requiring direct access to them at the time of observation (e.g., Zentall, Sutton, & Sherburne, 1996).

To avoid positional biases, we randomized the location (left or right side) of the red and blue dishes and then randomly placed the robot in front of one of them. Similarly, we used a randomized block design to avoid order effects. Half of the chicks saw the pecking robot on the first day and the scanning robot on the second, and the other half experienced the reverse sequence. On the third day, we conducted a test trial to evaluate whether experience of the robot in association with a distinctively colored dish had inculcated a feeding preference. Chicks were presented with one blue and one red dish, each containing corn, separated by 30 cm. Positions were randomly determined, as during training trials. The interval between training trials was 22–29 hr.

Setting up the robot, dishes, and fence in a pen took between 4 and 6 min. The experimenter then retreated to an adjacent hiding place and recorded the chick’s behavior, starting 30–60 s after she had left the aviary. High-resolution footage of behavior was obtained by tracking chicks with a digital color video camera (Panasonic NV-DS 15).

Response Measures and Analysis

Video analyses yielded frequency scores for social behavior, which was assigned to one of the following six categories:

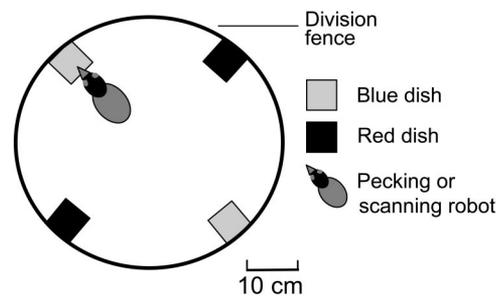


Figure 1. Plan view of the experimental setup. During training trials, the robot demonstrator was placed randomly adjacent to either the red or the blue dish. The position of the other dishes was also assigned randomly (see Method section). All dishes contained corn. The division fence (present during training only) prevented chicks from eating the corn but enabled them to peck at the edge of the dishes through the fence.

- (a) *Approach only*: Chick approached the fence to within 30 cm and then left the area again, without feeding or showing interest in the dishes.
 - (b) *Feeding*: Pecking and scratching within a 30-cm circumference around the fence.
 - (c) *Pecking at fence*: Chicks pecked at the fence within 10 cm on either side of a dish.
 - (d) *Pecking at dish*: Chicks pecked at the outside of a dish through the fence.
 - (e) *Pushing*: Chick pushed against the division fence within 10 cm on either side of a dish.
- For analysis, responses c through e were combined as “interest in dishes.”
- (f) *No response*: Behavior could not be assigned to any of the above categories.

For statistical analysis, we used the duration of feeding—the only behavioral state recorded—and latency to the first approach. All other behaviors were brief events for which frequency scores were more appropriate. Behaviors including pecking characteristically occurred in bouts, so these were counted instead of the individual movements. Bouts were operationally defined as having ended when 3 s passed without further pecking.

Exploratory analysis revealed considerable heterogeneity of variance, and data transformation did not usually generate normality. We thus used nonparametric tests (two-tailed) for all pairwise comparisons. The alpha level was .05 throughout.

Results

Overall Response to the Pecking and Scanning Robot

Table 1 summarizes the overall pattern of responses in all three trials. During the training sessions on the first and second day, the proportion of chicks responding was higher when the demonstrator was a pecking robot than when it was a scanning one (Table 1a); $\chi^2(1, N = 40) = 4.27, p = .04$. Feeding duration was also significantly greater during the “pecking trials” (Table 1b); Wilcoxon signed-ranks test, $z = -2.44, n = 40, p = .02$, although latency to respond to the two types of robot was similar (Table 1c); Wilcoxon signed-ranks test, $z = -0.10, n = 40, p = .92$.

Chicks that approached the robots tended to show an interest in the dishes (i.e., they pushed against the fence directly in front of the dishes, pecked at that fence, or pecked at the dishes through the fence; Table 1d). A smaller proportion either only approached the area within 30 cm around the fence before retreating again, or only spent time feeding (scratching in the leaf litter and pecking) within that area (Table 1d).

Positional Preferences During Training Sessions

Figures 2a and 2b illustrate results for all chicks that showed an interest in the dishes. Data are presented for both the initial response observed in each training session (Figure 2a) and the overall level of interest recorded during the 20-min session (Figure 2b). Sample sizes varied because the number of chicks that responded to each type of stimulus varied, and of these chicks, different numbers of individuals showed an actual interest in the dishes (compared with approach only and feeding [<30 cm] only; Table 1). The leftmost bars in both panels represent interest shown by the chicks in dishes of the same color as that the robot appeared to feed from (“robot dish”). For the training sessions, this is further subdivided into responses to the robot dish and those to the second, identically colored, dish away from the robot (see Figure 1). We conducted this analysis because we wished to test whether the chicks might be reluctant to approach the robot closely, which could have produced an artifactual reduction in apparent preference for dishes of the color indicated. There was no evidence of such an effect when only the first approach to the robot was considered (Binomial tests: pecking: $p = .27, n = 13$; scanning: $p = .69, n = 6$). We therefore pooled data for the initial response to “same color” dishes for further analysis.

However, the effect of having a robot close to one of the dishes approached significance in analyses of overall interest in containers of a particular color (Wilcoxon signed-ranks test: pecking: $p = .07, z = -1.79, n = 13$; scanning: $p = .06, z = -1.90, n = 6$). Chicks thus showed a tendency to avoid the robot dish. To account for this effect, we conducted two types of analysis for the results presented below. First, we pooled all data for pecks at the same color dishes, thus including those at the robot dish. Second, we considered only pecks at the dish of the same color away from the robot and compared this total with the mean value for the two differently colored dishes.

Preference for Dish Color During Training Sessions

During the training session, chicks watching a pecking robot were attracted to a dish of the same color. This trend approached significance when only the initial response was considered (Figure 2a, binomial test, $p = .10, n = 18$) and was unambiguously significant when overall frequency was scored, in both types of analysis described above (Figure 2b, Wilcoxon signed-ranks test,

Table 1
Summary of Responses During Training Sessions (Day 1 and 2 of the Experiment) and the Preference Test (Day 3)

Stimulus	Day	(a) % chicks with response	(b) Time spent feeding <30 cm of fence (s)		(c) Latency to first response (s)		(d) Type of response (% chicks)		
			Mdn	25th, 75th percentiles	Mdn	25th, 75th percentiles	Approach only	Feeding (<30 cm) only	Interest in dishes
Pecking robot	1 or 2	73	30	0, 243	120	10, 480	14	24	62
Scanning robot	1 or 2	50	0	0, 60	210	105, 495	10	15	75
Test (dishes only)	3	48	—	—	30	5, 360	0	—	100

Note. $N = 40$ chicks. Dashes indicate that the values were not measured because chicks and dishes were not separated by a fence during the preference test.

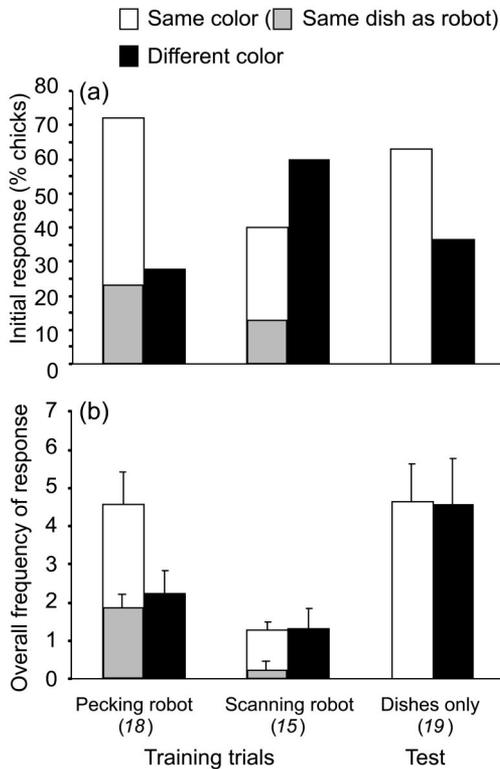


Figure 2. Response to the pecking or scanning robot during training trials (Days 1 and 2) and to dishes only during the preference test on Day 3. Results are shown for both the frequency of initial response (Figure 2a) and the mean frequency of responses during the 20-min observation period (+SE; Figure 2b). Data for interest in dishes of the same color as that adjacent to the robot are subdivided into responses to the dish closest to the robot (gray bar) and responses to an identical dish on the other side of the arena (white bar). The bars for different color represent the pooled responses to control dishes. Numbers in brackets show sample sizes.

responses to same color pooled: $p = .01$, $z = -2.58$, $n = 18$; robot dish excluded: $p < .01$, $z = -2.73$, $n = 18$).

In contrast, the scanning robot failed to evoke such a preference. Chicks in these trials divided their interest in dishes equally between the two colors, both in their initial response (Figure 2a, binomial test, $p = .61$, $n = 15$) and in overall responses (Figure 2b, Wilcoxon signed-ranks test, responses to same color pooled: $p = .84$, $z = -0.20$; robot dish excluded: $p = .23$, $z = -1.20$; both $ns = 15$).

Preference for Dish Color During Test Sessions

When presented with a choice between blue and red dishes 24 hr after the last training trial, chicks showed no detectable tendency to maintain the preference that they had previously shown during the training sessions (Figures 2a and 2b; “test”). There was no significant preference for the robot dish, either in the initial response (Figure 2a; binomial test, $p = .36$, $n = 19$) or when overall frequency was considered (Figure 2b; Wilcoxon signed-ranks test, $p = .10$, $z = -0.44$, $n = 19$). Almost half of the chicks showed no interest in the dishes at all (Table 1a).

We estimated effect size for overall frequency—which had produced the strongest evidence of preference during training—using Cohen’s method (Cohen, 1988). The resulting value ($d = 0.07$) suggests that the probability of Type II error in our analyses of test trial behavior is extremely low.

Analyses of the pooled data from all subjects do not consider the order of training experiences, which were counterbalanced. It was hence logically possible that the nonsignificant overall result masked a primacy effect (i.e., learning only when the pecking robot was seen first) or a recency effect (i.e., expression of a preference only when the pecking robot had been seen second). We therefore tested for the formation of a preference in each of these two subgroups separately but found none. Chicks that saw the pecking robot first showed no significant tendency to approach the dish indicated (initial response: binomial test, $p = .73$, $n = 8$; overall responses: Wilcoxon signed-ranks test, $p = .78$, $z = -2.82$, $n = 8$). Similarly, the chicks that encountered the pecking robot on the second day of training showed no significant preference (initial response: binomial test, $p = .55$, $n = 11$; overall responses: Wilcoxon signed-ranks test, $p = .84$, $z = -2.04$, $n = 11$).

Discussion

Two-day-old, naive brush-turkey chicks showed increased interest in a distinctively colored dish when they observed a robot pecking at food in a dish of the same color (see Figure 2). This immediate response was evoked strongly by simulated foraging behavior but not by the control scanning robot. Social facilitation would offer a parsimonious explanation for a general increase in feeding activity (Zajonc, 1965; Evans & Marler, 1994), but this simple process cannot account for the strong tendency of chicks to select a dish of the same color as that in front of the robot. Choice dishes had no reliable spatial relationship with the robot dish, so our results also cannot be due to local enhancement (Thorpe, 1963). Chicks thus seem to have expressed a socially transmitted feeding preference during training, but this effect proved ephemeral. We could detect no trace of tendency to feed from the dish that had been indicated by the robot when chicks were tested 24 hr or 48 hr later (see Figure 2). Our results hence provide no evidence for social learning, which is characterized by the stable performance of learned behavior for much longer periods (Galef & Giraldeau, 2001).

These findings contrast with those obtained in studies of social galliforms, such as chickens and jungle fowl (see introduction). Hatchlings of this species acquire lasting food preferences after observing the feeding behavior of an adult hen (Bartashunas & Suboski, 1984) or same-age companions (McQuoid & Galef, 1992). The sequence and timing of training and test sessions in our experiments were based on those used in studies that have demonstrated robust social learning in fowl (McQuoid & Galef, 1992), suggesting that brush-turkeys fail to acquire feeding preferences under comparable conditions.

However, chicks in our experiments were 3–4 days old when first trained compared with the 21- to 28-day-old Burmese fowl chicks tested by McQuoid and Galef (1992). Fowl chicks are known to be capable of acquiring lasting food preferences in the first few days of life (Bartashunas & Suboski, 1984), but the difference in chick age between the present study and previous

work nevertheless limits our ability to make direct comparisons. In addition, the chicks used by McQuoid and Galef (1992) were raised in groups, with opportunities to engage in social learning, whereas our brush-turkey hatchlings were socially naive when experiments commenced.

An exhaustive test for social learning in brush-turkeys would hence require additional studies in which the effects of chicks' age and social experience were fully explored. Ideally, such experiments would include a comparison group of fowl chicks, maintained and tested under identical conditions. It would also be valuable to examine the possibility that differences between our results and those of other studies are attributable to more rapid forgetting in brush-turkeys, for example, by reducing the interval between training and test trials.

Direct comparisons with other galliforms are also complicated by likely differences in maturation rates. To our knowledge, there are no studies designed to evaluate growth rate in brush-turkeys and chickens, but comparisons with peacocks, *Pavo cristatus*, and ring-necked pheasants, *Phasianus colchicus*, show that brush-turkeys are larger at hatching, but then grow more slowly, than these related species (Starck & Sutter, 2000). It would thus be interesting to conduct tests of learning in brush-turkeys and chickens that matched the two species for maturational stage, rather than chronological age. This approach would control for potential differences in sensory and social development.

Whereas it would be premature to conclude that brush-turkey chicks are incapable of learning from conspecifics under any conditions, it is nevertheless interesting to evaluate our results in the context of differences in life history. Recall that megapodes are highly unusual because chicks do not form bonds with their parents (Jones, Dekker, & Roselaar, 1995). In addition, chicks hatch asynchronously from incubation sites—which are typically widely distributed—and then quickly disperse into dense vegetation (Göth & Vogel, 2002a, 2002b, 2003). Opportunities to learn from conspecifics hence arise rarely and unpredictably. This essentially solitary development contrasts greatly with that of social galliforms, such as chickens and jungle fowl, which are reared by their mother and surrounded by siblings throughout early life. In particular, if social learning were to occur in brush-turkeys, then the fitness benefit conferred by occasional enhancement of foraging efficiency would likely be small. This idea is consistent with the conclusion that social transmission of preferences is most common in group-living species, especially if these compete for food, and that it is less evident, or even absent, in solitary species (Lefebvre & Giraldeau, 1996).

Our results also raise the question of whether the apparent lack of social learning in brush-turkeys reflects a more general insensitivity to experiential factors. Studies conducted to date suggest that this is unlikely to be true. Newly hatched brush-turkeys quickly identify suitable food items using trial and error learning (Göth & Proctor, 2002), although the stability of the resulting preferences has not yet been measured. In contrast, anti-predator behavior seems to be based on predispositions, as it is expressed immediately after hatching, without previous experience (Göth, 2001). Chicks also express most of their repertoire of social behavior during their first interaction with similar-age conspecifics (Göth & Jones, 2003). These results do not imply that the development of behavior requires no social or other experience but

rather hint at a strong interplay between inherited factors and individual learning.

Understanding the factors responsible for the observed distribution of social learning in galliforms will require a far greater number of quantitative analyses than are currently available, a point that has been made more generally in several reviews of current theoretical models (Dukas, 1998; Laland, Richerson, & Boyd, 1996). We suggest that it will be valuable to test for social learning at different ages, under different rearing conditions, and in other functional contexts, such as habitat and mate choice. Comparisons among closely related species with divergent life histories have the potential to reveal the interplay between social, ecological, and metabolic constraints in the evolution of learning.

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Call for Nominations

The Publications and Communications (P&C) Board has opened nominations for the editorships of **Behavioral Neuroscience**, **JEP: Applied**, **JEP: General**, **Neuropsychology**, **Psychological Methods**, and **Psychology and Aging** for the years 2008–2013. John F. Disterhoft, PhD; Phillip L. Ackerman, PhD; D. Stephen Lindsay, PhD; James T. Becker, PhD; Stephen G. West, PhD; and Rose T. Zacks, PhD, respectively, are the incumbent editors.

Candidates should be members of APA and should be available to start receiving manuscripts in early 2007 to prepare for issues published in 2008. Please note that the P&C Board encourages participation by members of underrepresented groups in the publication process and would particularly welcome such nominees. Self-nominations also are encouraged.

Search chairs have been appointed as follows:

- **Behavioral Neuroscience:** Linda P. Spear, PhD, and J. Gilbert Benedict, PhD
- **JEP: Applied:** William C. Howell, PhD
- **JEP: General:** Peter A. Ornstein, PhD
- **Neuropsychology:** Susan H. McDaniel, PhD, and Robert G. Frank, PhD
- **Psychological Methods:** Mark Appelbaum, PhD
- **Psychology and Aging:** David C. Funder, PhD, and Leah L. Light, PhD

Candidates should be nominated by accessing APA's EditorQuest site on the Web. Using your Web browser, go to <http://editorquest.apa.org>. On the Home menu on the left, find Guests. Next, click on the link "Submit a Nomination," enter your nominee's information, and click "Submit."

Prepared statements of one page or less in support of a nominee can also be submitted by e-mail to Karen Sellman, P&C Board Search Liaison, at ksellman@apa.org.

Deadline for accepting nominations is **January 20, 2006**, when reviews will begin.