

- WOLFSON, A. 1952. The cloacal protuberance—A means for determining the breeding condition in live male passerines. *Bird-Banding* 23:159–165.
- WOLFSON, A. 1954a. Notes on the cloacal protuberance, seminal vesicles, and a possible copulatory organ in male passerine birds. *Bulletin of the Chicago Academy of Sciences* 10:1–23.
- WOLFSON, A. 1954b. Sperm storage at lower-than-body temperature outside of the body cavity in some passerine birds. *Science* 120:68–71.
- WOLFSON, A. 1960. The ejaculate and the nature of coition in some passerine birds. *Ibis* 102:124–125.

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Observational Learning in Hummingbirds

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ABSTRACT.—Migratory hummingbirds forage on diverse assemblages of flowers varying in shape, color, and accessibility. Do hummingbirds learn to feed from flowers by observing other hummingbirds? Learning abilities of Ruby-throated (*Archilochus colubris*), Broad-tailed (*Selasphorus platycercus*), and Rufous (*S. rufus*) hummingbirds were studied in the presence or absence of a knowledgeable tutor. In two sequential trials hummingbirds learned to feed from artificial feeders of increasing complexity. Feeders in the first trial had easy access and were colored red at the nectar spout. In this initial trial, hummingbirds attempted to feed from the artificial feeder regardless of tutor presence, but tutored birds learn to feed more quickly. Feeders in the second trial were uncolored and the nectar spout was surrounded by a long artificial corolla. Tutored birds again learned to feed more quickly than their solitary counterparts. However, both untutored and tutored hummingbirds learned to feed more quickly in the second trial than the first, suggesting that the initial task of identifying a novel feeding resource is more difficult than learning how to access an identified resource.

Animals that easily learn how to use novel food resources can quickly adapt to novel environments (Greenberg 1989) and are more likely to be able to cope with urbanization (Sasvári 1979). The adoption of novel food resources is facilitated by the ability to learn through observations of animals feeding from those resources. That behavior, termed observational learning, applies to any problem-solving situation in which an animal that has viewed an experienced

demonstrator learns a behavior more quickly than an animal that has not (Davey 1981). Observational learning can lead to the rapid spread of a new foraging behavior, such as the opening of milk bottles by Tits (genus *Parus*) in Great Britain (Fisher and Hinde 1949, but see Sherry and Galef 1984, 1990).

North American migratory hummingbirds consume flower nectar from a large number of plant species across their considerable wintering and breeding ranges (Grant and Grant 1968). For example, the Rufous Hummingbird (*Selasphorus rufus*) reaches its northern range limit of southern Alaska during the summer breeding season and its southern limit of southern Mexico during the winter (Calder 1993). Throughout the range of hummingbirds, the flowers they pollinate are typically displayed according to the “hummingbird flower syndrome” (Feinsinger 1987) classified as primarily red, tubular flowers. However, North American migratory hummingbirds also feed from flowers that are neither tubular nor red (Grant and Grant 1968) including flowers with white, free-petals and unfused corollas such as *Eucalyptus* spp.

Presence of nectar in different flowers must be learned at two critical stages of a migratory hummingbird's life history: at fledging and during the first migration cycle. Fledgling hummingbirds follow their mother for several weeks after leaving the nest and eventually learn to feed from the same flowers that she does (Schuchmann 1999). The mode of floral learning by fledgling hummingbirds is not known, but observational learning is a likely candidate. After fledging, North American hummingbirds undergo considerable migrations during which time they are again forced to learn new flowers at each stage of the round-trip journey back to the breeding habitat. In addition, year-to-year variation in flower abundance will probably result in selection for learn-

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ing beyond the first year and at other periods of the migratory cycle. During breeding, migration, and winter residency, Nearctic–Neotropical hummingbird migrants forage and compete in mixed-species assemblages (Des Granges 1979, Kodric-Brown and Brown 1978), suggesting that hummingbirds may observe the feeding behavior of both conspecifics and heterospecifics.

Studies of observational learning are most illustrative when the precise effects of the tutor on the subject's behavior can be quantified and interpreted in the context of the subjects' natural history (Alcock 1969). Behaviors that are copied from a tutor can result in social facilitation whereby the behavioral effect of an observation is transitory and then terminated following the removal of the tutor (Klopfer 1961). After the removal of the tutor, persistence of the behavior distinguishes observational learning from social facilitation (Alcock 1969). The object of this study was to test three predictions: (1) Hummingbirds learn to feed from novel resources more quickly in the presence of a knowledgeable tutor. (2) The use of a novel floral resource by hummingbirds continues in the absence of a tutor. (3) Observational learning is more important for novel food sources than modified versions of previously encountered resources.

Methods.—The study was conducted with four female and seven male Ruby-throated Hummingbirds (*Archilochus colubris*) mist-netted in Bastrop County, Texas, and one female Rufous (*S. rufus*) and two male Broad-tailed (*Selasphorus platycercus*) hummingbirds captured in Jeff Davis County, Texas, in September and October of 1998. Birds were housed in screen cages (dimensions: 90 × 90 × 90 cm) and were fed with adult hummingbird feed solution containing sucrose, lipids, proteins, and fiber (Roudybush, Sacramento, California). Two or three birds were housed together within one cage. Hummingbird care was in accordance with federal and state guidelines.

After capture, naïve birds were allowed to acclimate to the lab for two days before experimental trials began. During the laboratory acclimation period, birds fed on the nectar solution from 120 mL hummingbird feeders with red bases and yellow bee guards. Naïve birds were visually separated from birds that had already gone through the learning trials.

Prior to the beginning of each trial, the birds were denied a meal for 30 min so that their crops were empty and they were presumably hungry (Roberts 1996). During the learning trials, nectar solution was presented to the hummingbirds in a 10 mL syringe. To ensure that birds did not starve before learning how to feed, we hand-fed all subjects approximately once every hour with the syringe until they learned to feed from it without aid.

The experiment was conducted in two sequential trials to measure the observational learning capacity

of hummingbirds. Trial 1 tested the ability of hummingbirds to learn to feed from a novel nectar source, the syringe. Trial 2 tested learning ability with a modified version of the syringe by covering the mouth with an artificial corolla. The experiment had two treatments: (1) In the solitary treatment, the hummingbirds were alone in the cage with only the feeder and perch. (2) In a tutored treatment, the hummingbird shared the cage with another hummingbird that had already learned to use the syringe for feeding. Each bird was tested in only one treatment and treatments were the same for each bird in both trials. During the experiment, we recorded two learning times, the time to first attempt, which was the first indication of interest in the syringe, and the time to first feeding, which was the first time the hummingbird fed from the syringe. The experiment began with solitary treatments so that birds could thereafter serve as tutors in the tutor treatments.

In trial 1, birds were placed in the cage with the syringe as the only nectar source. To aid the hummingbird in the identification of the syringe as a new resource, a small piece of red fabric was placed near the end of the syringe to provide a visual cue resembling a hummingbird flower. For tutor treatments we also looked for any defense activity by the tutor to protect the syringe.

Following the exposure to a novel resource in trial 1, birds spent several days in isolation and were given the syringe with the red cloth as their only food. During this time, their feeding behavior was periodically observed to confirm that birds continued to use the novel resource. Trial 2 was then performed to test for observational learning at a slightly modified resource. Access to the syringe was partially impeded by adding a clear plastic, wide mouth mask that resembled the shape of a flower corolla. The artificial corolla did not have any attached red cloth or additional cues. Treatments (tutor vs. no tutor) and protocols were the same as in trial 1.

Tutoring of the *Archilochus colubris* individuals was performed by conspecifics. The *Selasphorus rufus* female was not tutored, but served as the tutor for the *S. platycercus* males.

The two response variables (time to first attempt and time to first feeding) were compared between treatment and trial effects using a two-way analysis of variance. Both variables were transformed as the square root of time + 1.

Results.—All hummingbirds learned to feed from a novel food resource. Two birds were not tested in trial 2 because they were mistakenly exposed to modified feeders in between trials.

The presence of the feeding tutor may have stimulated more interest in the syringe because the average time required to make the first feeding attempt was shorter when compared to solitary birds (Fig. 1A). However, that difference (treatment effect) was not significant (Table 1). The average time required

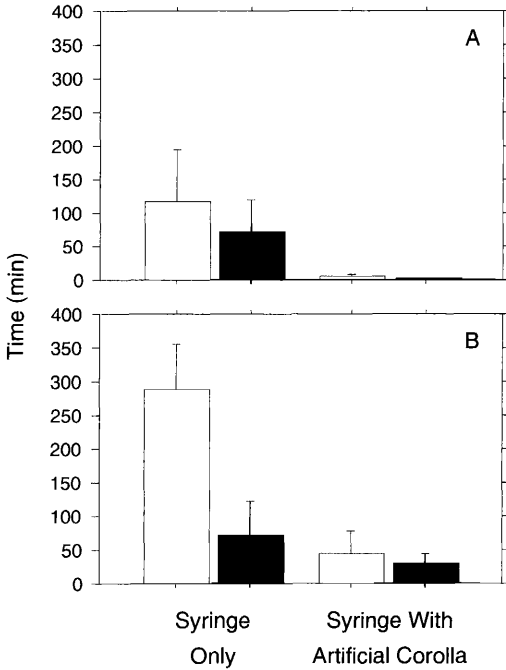


FIG. 1. Time required to learn nectar sources without and with a knowledgeable tutor. (A) The time to make the first attempt (first indication of interest) at using the nectar resource. White columns represent birds without a tutor, and black columns are for birds with tutors. Bars above the columns are standard errors about the mean. (B) Time to first feeding (learning the task) from the novel nectar resource. Shading and bars as above.

to make the first attempt at the feeding resource was significantly higher when the birds first encountered the syringe than when the syringe was later modified with the artificial corolla (trial effect). Thus, the initial task of identifying the syringe as a nectar resource was more difficult than recognizing an uncolored and slightly impeded version of it.

The time to first feeding (i.e. learning the task) was also significantly shorter in trial 2 after the birds had learned that the syringe contained artificial nectar (Fig. 1B). However, feeding time was also signifi-

cantly affected by the presence of a tutor such that tutored birds fed much sooner (Table 1). In addition, no interaction effects were found indicating that the tutored birds at the uncolored, artificial corolla learned more quickly than both untutored birds in trial 2, and when compared to their own performance in trial 1.

Of the seven birds without tutors in trial 1, six of those required hand feeding whereas only two of the seven tutored birds required hand feeding before learning the task. During trial 2, only one of the untutored birds required hand-feeding, whereas all of the tutored birds learned to feed within 1 h and thus did not require hand feeding. All hummingbirds were hand-fed with the same frequency, thus eliminating any bias between treatments.

After learning to feed at either novel or modified feeders, all hummingbirds continued to successfully use those resources. Furthermore, none of the birds engaged in territorial activity during the experiments although after several weeks in captivity birds became more accustomed to the laboratory environment and started to defend the syringes.

Discussion.—Because hummingbirds learned to feed from a novel nectar resource more quickly in the presence of a tutor, we conclude that hummingbirds use observational learning. In trial 1, the hummingbirds were able to associate the syringe (an artificial structure for nectar delivery) with a nectar resource more quickly if con- and heterospecific tutors were present. In trial 2, the birds did not require tutors to learn to feed from a syringe covered with a corolla. Thus, hummingbirds may rely on both conspecifics and heterospecifics to learn new floral resources, but on their own will probe a modified floral structure if nectar has been found in an alternate form of that structure.

Animals that learn quickly, and in a social context, can more easily adapt to changing environments. A comparison between tamed and untamed Budgerigars (*Melopsittacus undulatus*) found that tamed birds learned more quickly from tutors than untamed ones birds (Dawson and Foss 1965). Hesitation or refusal to feed from unfamiliar food sources (neophobia) is more common among birds with specialized as opposed to generalized foraging behavior (Greenberg 1984). Neophobic bird species also do not adapt well

TABLE 1. Effects of tutors on the speed of learning a novel feeder type. Data were transformed as the square root of time + 1.

Source	Time to first attempt				Time to first feeding		
	df	MSE	F	p	MSE	F	p
Trial	1	149.477	4.631	0.0426	228.077	6.892	0.0155
Treatment	1	7.789	0.241	0.6281	163.474	4.940	0.0368
Trial × treatment	1	0.918	0.028	0.8676	128.021	3.869	0.0619
Error	22	32.276			33.093		

to human-modified habitat compared to inquisitive and exploitative species (Greenberg 1989). Thus, more urbanized, curious species such as Great Tits (*Parus major*) and Rock Doves (*Columba livia*) are more likely to exhibit observational learning than are habitat specialists such as Greenfinches (*Chloris chloris*), Blue Tits (*P. caeruleus*), and Marsh Tits (*P. palustris*) (Klopfer 1961, Sasvári 1979, Lefebvre et al. 1997).

The incidence of observational learning in Ruby-throated, Broad-tailed, and Rufous hummingbirds in this study fits the observation that North American hummingbirds do well in human-modified habitats. In contrast, many tropical hummingbird species do not readily use hummingbird feeders (D. L. Altshuler pers. obs.). It would be worthwhile to examine the exploitative behavior of the 27 species of vulnerable or endangered hummingbirds (Collar et al. 1994) in a phylogenetic context. It would also be necessary to determine if their sensitivity to habitat modification is related to neophobia or simply to the inability to learn a novel resource. In the former case, birds would avoid a novel resource whereas in the latter case, birds would not avoid the object but would ignore it.

Predictors of use of observational learning include the social structure and territorial behavior of the species in question. A comparison between territorial and group feeding populations of Zenaida Doves (*Zenaida aurita*) revealed that territorial doves learned more readily from heterospecific tutors whereas group-foraging doves learned primarily from conspecifics (Dolman et al. 1996). Doves from a Zenaida population that experiences both territorial defense and group foraging learned as readily from conspecifics as heterospecifics (Carlier and Lefebvre 1997). An interspecific comparison between a population of territorial Zenaida doves and group-foraging feral pigeons (*Columba livia*) found a much greater propensity for learning in the pigeons, but that was the case for both social and nonsocial learning (Carlier and Lefebvre 1996).

Both tutored and untutored birds in our study quickly learned to use a modification of a previously encountered resource, suggesting that learning ability is more critical for a more novel resource. Learning to feed from a modified version of previously encountered resources has also been tested among three species of tits (*Parus* spp.) with a similar result: birds learn more easily, regardless of tutor presence, when they have already been exposed to a problem-solving situation (Sasvári 1985).

The hummingbirds in our study learned a novel food source more easily when tutored by a knowledgeable tutor. The behavior persisted after the removal of the tutor, indicating that the hummingbirds used observational learning as opposed to social facilitation. The benefits of using observational learning to hummingbirds include: (1) fledgling birds can

more easily learn floral food sources from their mother; (2) migrating hummingbirds can more easily learn novel food sources that they may only use once or twice in their lifetime; and (3) ability to find food sources in novel habitats such as human-modified habitat is enhanced. The learning ability and concordant habitat plasticity of some hummingbirds may explain their survival success despite loss of natural habitat.

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LITERATURE CITED

- ALCOCK, J. 1969. Observational learning by Fork-tailed Flycatchers (*Muscivora tyrannus*). *Animal Behaviour* 17:652–657.
- CALDER, W. A. 1993. Rufous Hummingbird (*Selasphorus rufus*) In *The Birds of North America*, no. 53 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.
- CARLIER, P., AND L. LEFEBVRE. 1996. Differences in individual learning between group-foraging and territorial Zenaida Doves. *Behaviour* 133:1197–1207.
- CARLIER, P., AND L. LEFEBVRE. 1997. Ecological differences in social learning between adjacent, mixing, populations of Zenaida Doves. *Ethology* 103:772–784.
- COLLAR, N. J., M. J. CROSBY, AND A. J. STATTERSFIELD. 1994. *Birds to Watch 2: The World List of Threatened Birds*. BirdLife International, Cambridge, United Kingdom.
- DAVEY, G. 1981. *Animal Learning and Conditioning*. Macmillan Education Ltd., London.
- DAWSON, B. V., AND B. M. FOSS. 1965. Observational learning in Budgerigars. *Animal Behaviour* 13:470–474.
- DES GRANGES, J.-L. 1979. Organization of a tropical nectar feeding bird guild in a variable environment. *Living Bird* 17:199–236.
- DOLMAN, C. S., J. TEMPLETON, AND L. LEFEBVRE. 1996. Mode of foraging competition is related to tutor preference in *Zenaida aurita*. *Journal of Comparative Psychology* 110:45–54.
- FEINSINGER, P. 1987. Approaches to nectarivore-plant interactions in the New World. *Revista Chilena de Historia Natural* 60:285–319.
- FISHER, J. AND R. A. HINDE. 1949. The opening of milk bottles by birds. *British Birds* 42:347–357.

- GRANT, K. G., AND V. GRANT. 1968. Hummingbirds and Their Flowers. Columbia University Press, New York.
- GREENBERG, R. 1984. Differences in feeding neophobia in the tropical migrant wood warblers *Dendroica castanea* and *D. pensylvanica*. *Journal of Comparative Psychology* 98:131–136.
- GREENBERG, R. 1989. Neophobia, aversion to open space, and ecological plasticity in Song and Swamp sparrows. *Canadian Journal of Zoology* 67:1194–1199.
- KLOPFER, P. H. 1961. Observational learning in birds: The establishment of behavioural modes. *Behaviour* 17:71–80.
- KODRIC-BROWN, A., AND J. H. BROWN. 1978. Influence of economics, interspecific competition, and sexual dimorphism on territoriality of migrant Rufous Hummingbirds. *Ecology* 59:285–296.
- LEFEBVRE, L., J. TEMPLETON, K. BROWN, AND M. KOELLE. 1997. Carib Grackles imitate conspecific Zenaida Dove tutors. *Behaviour* 134:1003–1017.
- ROBERTS, W. M. 1996. Hummingbird's nectar concentration preferences at low volume: The importance of time scale. *Animal Behaviour* 52:361–370.
- SASVÁRI, L. 1979. Observational learning in Great, Blue, and Marsh tits. *Animal Behaviour* 27:767–771.
- SASVÁRI, L. 1985. Different observational learning capacity in juvenile and adult individuals of congeneric bird species. *Zeitschrift für Tierpsychologie* 69:293–304.
- SCHUCHMANN, K. L. 1999. Family Trochilidae (Hummingbirds). Pages 468–680 in *Handbook to the Birds of the World*, vol. 5 (J. del Hoyo, A. Elliott, and J. Sargatal, Eds.). Lynx Edicions, Barcelona, Spain.
- SHERRY, D. F., AND B. G. GALEF, JR. 1984. Cultural transmission without imitation: Milk bottle opening by birds. *Animal Behaviour* 32:937–938.
- SHERRY, D. F., AND B. G. GALEF, JR. 1990. Social learning without imitation: more about milk bottle opening by birds. *Animal Behaviour* 40:987–989.

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Phylogenetic Utility of Avian Ovomuroid Intron G: A Comparison of Nuclear and Mitochondrial Phylogenies in Galliformes

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ABSTRACT.—A novel nuclear marker, the avian ovomuroid intron G (OVOG) was sequenced from 19 galliform taxa. Results of the phylogenetic analyses using OVOG were compared to those obtained using the mitochondrial cytochrome *b* (*cytb*) gene to determine the phylogenetic utility of OVOG. OVOG appeared to have strong phylogenetic signal for reconstructing relationships among genera and families, and the only difference between OVOG and *cytb* was in the placement of the New World quail (Odontophoridae). Genetic distances estimated using OVOG are approximately half of those estimated using *cytb*, although that relationship was not linear. OVOG exhibited patterns of nucleotide substitution very different from *cytb*, with OVOG having little base compositional

bias, a relatively low transition–transversion ratio, and little among-site rate heterogeneity.

Mitochondrial DNA (mtDNA) sequences are commonly used to estimate vertebrate phylogenies. MtDNA markers evolve rapidly, making investigation among closely related species possible, yet also contain enough slowly evolving sites to resolve deeper relationships. Although mtDNA phylogenies are likely to be correct in many cases (Moore 1995), use of mtDNA sequences can be problematic. MtDNA rarely undergoes recombination (Wolstenholme 1992), so problems due to lineage sorting or introgression cannot be detected. Nuclear pseudogenes of mtDNA sequences can also confound phylogenetic estimation (Sorenson and Quinn 1998). Therefore, it is useful to compare mtDNA phylogenies with nuclear gene phylogenies to control for such problems.

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