

- breeding success in Common and Roseate terns. *Bird-Banding* 43:97-106.
- NUR, N. 1984. The consequences of brood size for breeding Blue Tits. I: Adult survival, weight change and the cost of reproduction. *J. Anim. Ecol.* 53:479-496.
- PEARSON, T. H. 1968. The feeding biology of seabird species on the Farne Islands, Northumberland. *J. Anim. Ecol.* 37:521-552.
- REYER, H.-U., AND K. R. WESTERTERP. 1985. Parental energy expenditure: A proximate cause of helper recruitment in the Pied Kingfisher *Ceryle rudis*. *Behav. Ecol. Sociobiol.* 17:363-369.
- RICKLEFS, R. E., AND S. E. WHITE. 1981. The growth and energetics of chicks of the Sooty Tern (*Sterns fuscata*) and Common Tern (*S. hirundo*). *Auk* 98:361-378.
- RICKLEFS, R. E., AND J. B. WILLIAMS. 1984. Daily energy expenditure and water turnover rate of adult European Starlings (*Sturnus vulgaris*) during the nesting cycle. *Auk* 101:707-716.
- RICKLEFS, R. E., D. D. ROBY, AND J. B. WILLIAMS. 1986. Daily energy expenditure of adult Leach's Storm-Petrels during the nesting season. *Physiol. Zool.* 59:649-660.
- TATNER, P. 1990. Deuterium and oxygen-18 abundance in birds: Implications for energetics studies. *Am. J. Physiol.* 258:R804-R812.
- TATNER, P., AND D. M. BRYANT. 1988. The doubly-labelled water technique for measuring energy expenditure. Pages 77-112 in *Techniques in comparative respiratory physiology—An experimental approach* (C. R. Bridges and P. J. Butler, Eds.). Cambridge Univ. Press, Cambridge.
- UTTLEY, J. 1991. The influence of food supply on the reproductive effort of Arctic Terns *Sterna paradisaea*. Ph.D. thesis, Univ. Glasgow, Glasgow, United Kingdom.
- UTTLEY, J. 1992. Food supply and the allocation of parental effort in Arctic Terns *Sterna paradisaea*. *Ardea* 80:83-91.
- UTTLEY, J., P. MONAGHAN, AND S. WHITE. 1989. Differential effects of reduced sandeel availability on two sympatrically breeding species of tern. *Ornis Scand.* 20:273-277.
- WIENS, J. A. 1984. Modelling the energy requirements of seabird populations. Pages 255-284 in *Seabird energetics* (G. C. Whittow, and H. Rahn, Eds.). Plenum, New York.
- WINKLER, D. W., AND G. S. WILKINSON. 1988. Parental effort in birds and mammals: Theory and measurement. Pages 185-216 in *Oxford surveys in evolutionary biology*, vol. 5 (P. H. Harvey, and L. Partridge, Eds.). Oxford Univ. Press, Oxford.

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Parental Recognition of Juvenile Begging Calls in the Florida Scrub Jay

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Previous research on parent-offspring recognition in birds suggests that acoustic recognition systems should be common in colonial species where unrelated young intermingle freely at early ages. Because the inability to recognize young in dense breeding colonies could result in parents neglecting their own offspring and caring for unrelated juveniles, natural selection would be expected to favor vocal recognition of offspring in colonial species (Davies and Carrick 1961, Beer 1970, Evans 1970, Buckley and Buckley 1972, Beecher 1981, Falls 1982, Colgan 1983).

The relationship between coloniality and vocal recognition of offspring has been explored most thoroughly in swallows. In two colonial species, the Bank

Swallow (*Riparia riparia*) and Cliff Swallow (*Hirundo pyrrhonota*), offspring leave the nest at around 18 days of age and form creches that contain many nutritionally dependent fledglings (Beecher 1981, Stoddard and Beecher 1983). Young develop individually distinctive "signature" calls prior to fledging, and parents learn to discriminate between the calls of their own young and those of other young (Burt 1977, Beecher et al. 1981, Stoddard and Beecher 1983, Loesche et al. 1991). However, in two species of non-colonial swallows, the Barn Swallow (*H. rustica*) and Northern Rough-winged Swallow (*Stelgidopteryx serripennis*), dependent young seldom intermingle with those from other broods, nestlings do not develop distinctive signature vocalizations, and vocal recognition of offspring is apparently absent (Medvin and Beecher 1986, Beecher 1990, Medvin et al. 1992, 1993).

The four species of swallows studied by Beecher and colleagues provided an excellent opportunity to

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compare parent-offspring vocal recognition in colonial and noncolonial members of the same family. A possible parallel situation involves the colonial Pinyon Jay (*Gymnorhinus cyanocephalus*) and its noncolonial relatives in the family Corvidae (Brown 1974). Balda and Balda (1978) noted that parental recognition of fledgling begging calls is a strong component of the Pinyon Jay social system. Once young birds leave the nest, they form large creches containing from 50 to 300 dependent juveniles. An analysis of the begging calls of older nestlings and fledglings has shown that call structure varies considerably among individuals, and playback experiments have shown that adult Pinyon Jays are able to recognize the calls of their own offspring by the time the young leave the nest to join the creche (McArthur 1982). Comparative data on parent-offspring recognition in noncolonial jays, however, are presently unavailable.

To contribute to the comparison of vocal recognition of offspring in colonial versus noncolonial birds, we describe an experimental study designed to determine whether adults of the Florida Scrub Jay (*Aphelocoma coerulescens coerulescens*), a noncolonial relative of the Pinyon Jay, can recognize the vocalizations of their own fledglings.

Methods.—The study was conducted at Archbold Biological Station in Highlands County, Florida, between late May 1991 and early July 1991. Several hundred Florida Scrub Jays reside on the station's 2,000-ha reserve and have been the focus of 25 years of research. The jay population had been color banded, and approximate territory locations and boundaries were mapped prior to the start of our study (Woolfenden and Fitzpatrick 1984, 1990, Mumme 1992, Schaub et al. 1992).

Florida Scrub Jays live in extended families comprising a monogamous breeding pair, their young, and one to several nonbreeding helpers. Nonbreeding helpers are usually relatives of the breeding pair that assist the pair by feeding and protecting nestlings and fledglings. Fledglings remain nutritionally dependent upon adults until 85 days of age. Florida Scrub Jays maintain continuously occupied territories that average about 9.0 ha per family. The nesting season lasts from mid-March to mid-June, and first clutches are laid by early April. Until mid-May, birds will renest if a first attempt fails (Woolfenden and Fitzpatrick 1984, 1990, McGowan and Woolfenden 1990).

Recordings of the begging calls of fledglings were made in the mornings between 0600 and 1200 EST on either the day of or the day prior to a playback experiment. A Marantz PMD-221 cassette tape recorder, TDK SA90 audio tapes (high bias) and a Sennheiser ME88 shock-mounted shotgun microphone were used to make all recordings. All fledglings were 35 to 65 days old when recorded. Sonagrams (wide band, sampling rate of 20 kHz) of the begging calls of eight different fledglings (Fig. 1) were made using

MacSpeech Lab II sound analysis software (GW Instruments).

Families with dependent fledglings were organized into 12 experimental units consisting of two families each (24 families total). The families in each experimental unit were at least two territories distant from each other. Recordings of the begging calls of fledglings were taken from both families, and were then played back to both families within the experimental unit. Each territory with young was recorded and used in only one experimental unit to avoid potential problems with pseudoreplication (Kroodsma 1989).

Because Florida Scrub Jays at Archbold are tame (Woolfenden and Fitzpatrick 1984), we were able to obtain recordings of fledglings at close range (<10 m). From recordings made in the field, 60 s of nearly continuous begging calls were then isolated to be used as the playback stimulus.

Playback experiments were performed in the mornings between 0600 and 1200. The taped calls were broadcast through Sony SRS-67 speakers, using the same recorder and audio tapes as before. A single speaker was concealed in vegetation 10 m away from the experimenter and both tapes were broadcast from it in turn. Speakers were always positioned well within a group's territory boundaries. For each of the two territories comprising an experimental unit, each of the two 60-s-long tapes was played with a 5-min time lapse in between. Therefore, each group within an experimental unit was presented with two playback stimuli; begging calls of familiar fledglings (offspring) and unfamiliar fledglings (nonoffspring). Tapes were played in random order determined by the flip of a coin. A playback began when both parents were within 10 m of the speaker, and the birds no longer seemed affected by our presence. The volume was adjusted by ear to approximate natural volume.

Three response variables were measured as follows: (A) time (in seconds) to first response, determined either by the production of vocalizations and/or approach toward the speaker; (B) distance of closest approach (in meters); and (C) number of flights over the speaker. The latter was recorded as: (0) none; (1) one to three; (2) four to six; and (3) seven or more. Separate measurements were made for both the male and female breeder in each of the above categories. Statistical analysis was conducted using analysis of variance (ANOVA) with either a repeated-measures design, or with a randomized-block design based on random block effects (Neter et al. 1990).

Results.—Our experimental design allows for many different ways to block for variances in ANOVA calculations. One approach is to block the results by individual bird in a repeated-measures design; that is, to compare the responses made by a single bird to the calls of familiar and unfamiliar fledglings. The data were blocked by individual breeder and subjected to a two-factor repeated-measures ANOVA us-

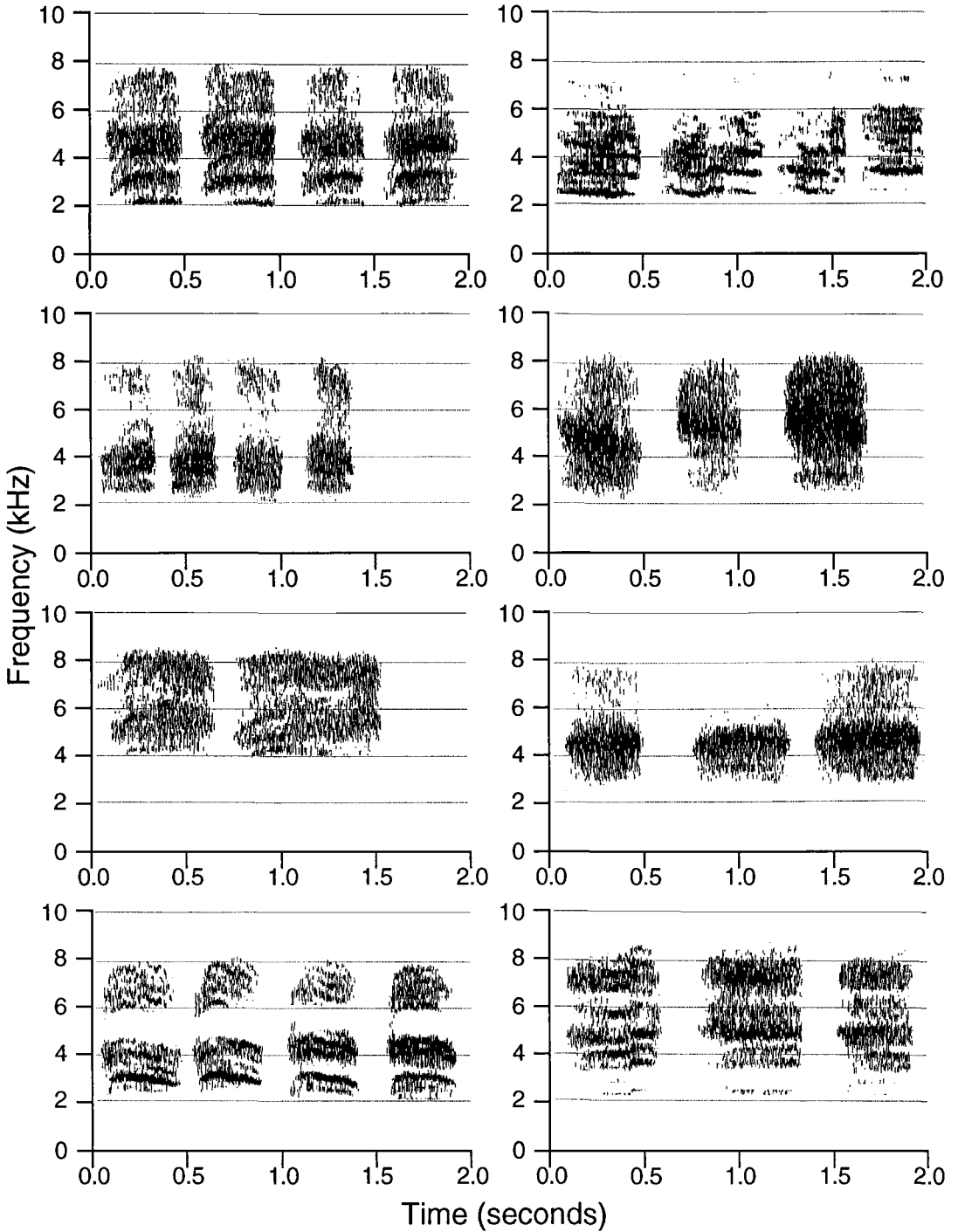


Fig. 1. Sonograms of the begging calls of eight different fledglings from eight different groups. Two to four calls shown for each individual.

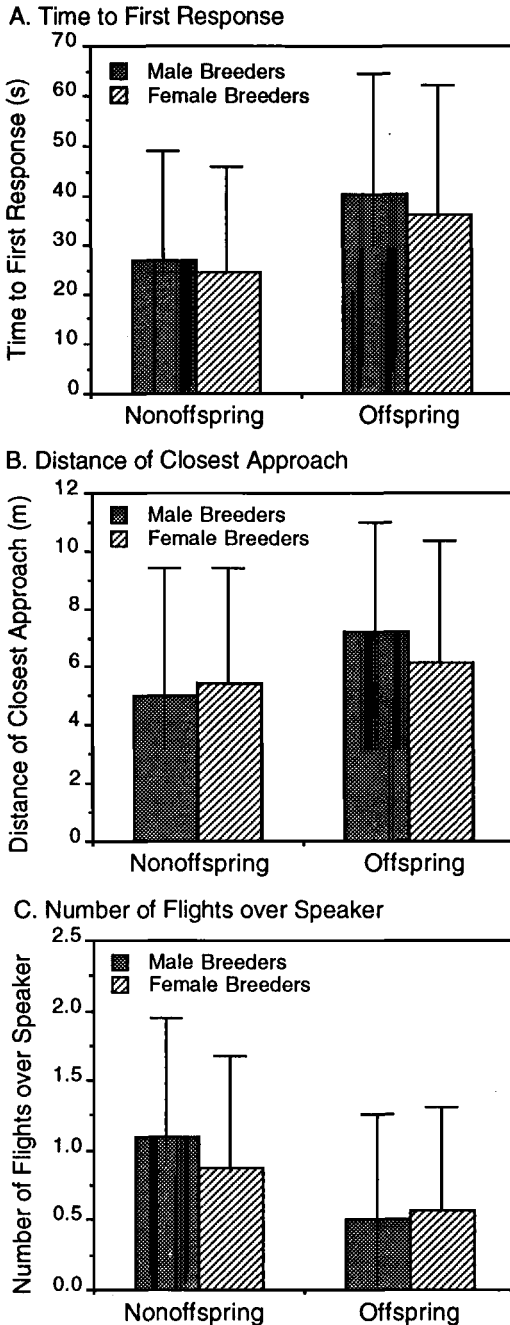


Fig. 2. Responses (\bar{x} with SD indicated by error bars) of breeding Florida Scrub Jays to playbacks of fledgling begging calls in relation to sex of breeder and familiarity of playback stimulus. Sample size in each familiarity category is 20 for males and 23 for females.

ing familiarity of the playback stimulus (offspring vs. nonoffspring) as a within-subjects factor and sex of the breeder (male vs. female) as a between-subjects factor. Complete data were available for 20 male and 23 female breeders. In general, time to first response and distance of closest approach increase with familiarity with the playback stimulus, while number of flights over the speaker decreases (Fig. 2). Familiarity had a significant effect on both time to first response and number of flights over the speaker, but not on distance of closest approach. Sex of the breeder, however, had no significant effect on any of the response variables measured. Interactions between sex and familiarity also were nonsignificant (Table 1).

A second approach is to block by playback stimulus (i.e. to compare responses to the same playback tape of birds differing in their familiarity to the stimulus). In this analysis, data were blocked by playback stimulus and subjected to a two-factor randomized-block ANOVA using familiarity and sex as factors. Complete data were available from 40 breeders (20 males and 20 females). The results of the ANOVA indicate that familiarity has a significant effect on time to first response and number of flights over the speaker, but not on distance of closest approach (Table 1). None of the response variables were significantly influenced by sex, or by the interaction between sex and familiarity (Table 1).

Discussion.—Our results indicate that parent Florida Scrub Jays discriminate between, and respond differently to, the begging vocalizations of their own young and those of other fledglings. This discrimination is evident both when contrasting the responses of the same breeder to different playback tapes, and when contrasting the responses of different breeders to the same playback stimulus (Table 1). Breeding jays respond more quickly and fly over the speaker more frequently when presented with the calls of nonoffspring. This ability to discriminate between the vocalizations of offspring and unfamiliar young is similar to that observed in Pinyon Jays (McArthur 1982) and in other colonially breeding species (Beecher 1990, Lessells et al. 1991).

However, the responses of Florida Scrub Jays and Pinyon Jays differ considerably in at least one important respect. When presented with a playback stimulus, Florida Scrub Jays in our study responded more vigorously to the calls of nonoffspring than to the calls of their own young (Fig. 2, Table 1). In contrast, McArthur (1982) found that Pinyon Jays respond most intensely to the call of their own young, and essentially ignore the begging calls of nonoffspring. Although this difference in response may seem puzzling, we believe that it is interpretable in light of the differences in the social organization of these two species. Pinyon Jays breed in dense colonies, and dependent fledglings frequently congregate in large creches. An adult Pinyon Jay, therefore, would be unlikely to respond (aggressively or otherwise) to the

TABLE 1. Summary of two-factor ANOVAs (F -value with P in parentheses) evaluating effects of familiarity (offspring vs. nonoffspring) and sex (male vs. female) on responses of breeders to playbacks.

Response variable	Familiarity	Sex	Familiarity \times sex interaction
Blocking by individual bird (df = 1 and 41 for each variable)			
Time to first response	9.15 (0.004)	0.33 (0.57)	0.06 (0.81)
Distance of closest approach	2.96 (0.09)	0.12 (0.73)	0.75 (0.39)
Number flights over speaker	8.61 (0.006)	0.20 (0.66)	0.92 (0.34)
Blocking by playback stimulus (df = 1 and 38 for each variable)			
Time to first response	6.43 (0.02)	1.51 (0.23)	0.06 (0.80)
Distance of closest approach	2.25 (0.14)	0.70 (0.41)	0.91 (0.34)
Number flights over speaker	6.55 (0.01)	0.00 (0.99)	0.73 (0.40)

calls of nearby young that are not its own. Florida Scrub Jays, however, are highly territorial (Woolfenden and Fitzpatrick 1984), and adults usually respond aggressively to unfamiliar intruders, including juveniles. Thus, we would expect Florida Scrub Jays to respond more vigorously to the calls of unfamiliar young than to the calls of their own offspring.

Our finding that Florida Scrub Jays can discriminate between the begging calls of their own offspring and those of unfamiliar young is unexpected in light of the fact that such discrimination abilities are usually absent in noncolonial species (e.g. Barn Swallows and Northern Rough-winged Swallows; Beecher 1990). However, even though Florida Scrub Jays are highly territorial, and young are at least partially dependent until 85 days of age, fledglings do not necessarily remain in their natal territory all the time. During the late summer, fledglings may wander onto adjacent territories and beg for food from any adult encountered. Such juveniles are only rarely fed by the residents territory owners, and are usually chased away (Woolfenden and Fitzpatrick 1984:153-154). Therefore, although fledgling Florida Scrub Jays do not congregate in large creches as do juveniles of Pinyon Jays and colonial swallows, limited intermingling of young does occur while young are still dependent upon their parents. This limited intermingling may have selected for vocal recognition of young in this noncolonial species. Alternatively, vocal recognition of young may simply reflect the presence of a generalized vocal recognition system in the Florida Scrub Jay, perhaps similar to the system responsible for neighbor-stranger vocal discrimination in many territorial songbirds (Falls 1982, Godard 1991).

Although Florida Scrub Jay breeders can distinguish between the vocalizations of their own young and those of unfamiliar young, our results suggest that their discrimination abilities are less well developed than those found in the Pinyon Jay. While McArthur (1982) documented dramatic, qualitative differences in the response of adult Pinyon Jays to the calls of offspring and unrelated young, we found only subtle and quantitative differences in the Florida

Scrub Jay (Fig. 2). One factor complicating a comparison of vocal recognition in these two species is differences in the design of the two studies. McArthur (1982) investigated parental recognition of 15- to 20-day-old nestlings, and our study focused on parental recognition of 35- to 65-day-old fledglings. However, because several studies have shown that vocal recognition of young typically improves with offspring age (e.g. Beecher et al. 1981, McArthur 1982), this is unlikely to explain the apparently weaker discrimination seen in the Florida Scrub Jay. Instead, we suggest that although the limited intermingling of young in the Florida Scrub Jay may provide some selection pressure for vocal recognition of young, selection is probably not as strong as it would be in a colonial species (such as the Pinyon Jay) whose dependent young regularly congregate in large creches. More detailed laboratory and field experiments are required to test this hypothesis (Loesche et al. 1991, Storey et al. 1992).

Although our study did not address either the ontogeny or acoustic basis of vocal recognition in the Florida Scrub Jay, examination of the sonagrams in Figure 1 suggests that sufficient interindividual variation exists in the acoustic properties of fledgling vocalizations to provide a basis for individual recognition. This in turn suggests that cross-fostering experiments would be useful in disentangling the genetic and environmental factors responsible for interindividual variation in fledgling vocalizations. Similarly, a more detailed analysis of vocal recognition in the Florida Scrub Jay, focusing on the development of interindividual variation in begging calls and the ontogeny of parental recognition, would provide additional insight into the proximate and ultimate causes of parent-offspring recognition in birds.

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LITERATURE CITED

- BALDA, J. H., AND R. P. BALDA. 1978. The care of young Pinyon Jays (*Gymnorhinus cyanocephalus*) and their integration into the flock. *J. Ornithol.* 119:146-171.
- BEECHER, M. D. 1981. Development of parent-offspring recognition in birds. Pages 45-66 in *Development of perception: Psychobiological perspectives*, vol. 1 (R. N. Aslin, J. R. Alberts, and M. R. Petersen, Eds.). Academic Press, New York.
- BEECHER, M. D. 1990. The evolution of parent-offspring recognition in swallows. Pages 360-380 in *Contemporary issues in comparative psychology* (D. A. Dewsbury, Ed.). Univ. Florida, Gainesville.
- BEECHER, M. D., I. M. BEECHER, AND S. HAHN. 1981. Parent-offspring recognition in Bank Swallows: II. Development and acoustic basis. *Anim. Behav.* 29:95-101.
- BEER, C. G. 1970. Individual recognition of voice in the social behavior of birds. *Adv. Study Behav.* 3:27-74.
- BROWN, J. L. 1974. Alternate routes to sociality in jays—With a theory for the evolution of altruism and communal breeding. *Am. Zool.* 14:63-80.
- BUCKLEY, F. G., AND P. A. BUCKLEY. 1972. Individual egg and chick recognition by adult Royal Terns (*Sterna maxima maxima*). *Anim. Behav.* 20:457-462.
- BURT, E. H., JR. 1977. Some factors in the timing of parent-chick recognition in swallows. *Anim. Behav.* 25:231-239.
- COLGAN, P. 1983. *Comparative social recognition*. Wiley Interscience, New York.
- DAVIES, S. J. F., AND R. CARRICK. 1961. On the ability of Crested Terns to recognize their own chicks. *Aust. J. Zool.* 10:171-177.
- EVANS, R. H. 1970. Parental recognition and the "mew" call in Black-billed Gulls. *Auk* 87:503-513.
- FALLS, J. B. 1982. Individual recognition by sound in birds. Pages 237-278 in *Acoustic communication in birds*, vol. 2 (D. E. Kroodsma and E. H. Miller, Eds.). Academic Press, New York.
- GODARD, R. 1991. Long-term memory of individual neighbours in a migratory songbird. *Nature* 350:228-229.
- KROODSMA, D. 1989. Suggested experimental designs for song playbacks. *Anim. Behav.* 37:600-609.
- LESSELLS, C. M., N. D. COULTHARD, P. J. HODGSON, AND J. R. KREBS. 1991. Chick recognition in European Bee-eaters: Acoustic playback experiments. *Anim. Behav.* 42:1031-1033.
- LOESCHE, P., P. K. STODDARD, B. J. HIGGINS, AND M. D. BEECHER. 1991. Signature versus perceptual adaptations for individual vocal recognition in swallows. *Behaviour* 118:15-25.
- MCCARTHER, P. D. 1982. Mechanisms and development of parent-young vocal recognition in the Pinyon Jay. *Anim. Behav.* 30:62-74.
- MCGOWAN, K. J., AND G. E. WOOLFENDEN. 1990. Contributions to fledgling feeding in the Florida Scrub Jay. *J. Anim. Ecol.* 59:691-707.
- MEDVIN, M. B., AND M. D. BEECHER. 1986. Parent-offspring recognition in the Barn Swallow (*Hirundo rustica*). *Anim. Behav.* 34:1627-1639.
- MEDVIN, M. B., P. K. STODDARD, AND M. D. BEECHER. 1992. Signals for parent-offspring recognition: Strong sib-sib call similarity in Cliff Swallows but not Barn Swallows. *Ethology* 90:17-28.
- MEDVIN, M. B., P. K. STODDARD, AND M. D. BEECHER. 1993. Signals for parent-offspring recognition: A comparative analysis of the begging calls of Cliff Swallows and Barn Swallows. *Anim. Behav.* 45:841-850.
- MUMME, R. L. 1992. Do helpers increase reproductive success? An experimental analysis in the Florida Scrub Jay. *Behav. Ecol. Sociobiol.* 31:319-328.
- NETER, J., W. WASSERMAN, AND M. H. KUTNER. 1990. *Applied linear statistical models*. Irwin, Homewood, Illinois.
- SCHAUB, R., R. L. MUMME, AND G. E. WOOLFENDEN. 1992. Predation on the eggs and nestlings of Florida Scrub Jays. *Auk* 109:585-593.
- STODDARD, P. K., AND M. D. BEECHER. 1983. Parental recognition of offspring in the Cliff Swallow. *Auk* 100:795-799.
- STOREY, A. E., R. E. ANDERSON, J. M. PORTER, AND A. M. MACCHARLES. 1992. Absence of parent-young recognition in kittiwakes: A re-examination. *Behaviour* 120:302-323.
- WOOLFENDEN, G. E., AND J. W. FITZPATRICK. 1984. *The Florida Scrub Jay: Demography of a cooperative-breeding bird*. Princeton Univ. Press, Princeton, New Jersey.
- WOOLFENDEN, G. E., AND J. W. FITZPATRICK. 1990. Florida Scrub Jays: A synopsis after 18 years of study. Pages 239-266 in *Cooperative breeding in birds: Long-term studies of ecology and behavior* (P. B. Stacey and W. D. Koenig, Eds.). Cambridge Univ. Press, New York.

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