TABLE 3. Number of eggs laid by captive Mallards.

Treatment	Clutch size													
	6	7	8	9	10	11	12	13	14	15	...	20	n	Mean
Control	2	3	2	1	1	—	—	—	—	—		—	9	7.6
Eggs removed	—	1	1	—	2	1	—	2	—	1		1	9	11.9

rie ducks, nor did egg additions decrease the number of eggs laid by Blue-winged Teal. Some captive Mallards of wild genetic stock did extend laying when eggs were removed from their nests. Thus, Mallard females have the physiological ability to produce excessive numbers of eggs, and some females can be induced to extend laying when food is freely available.

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Experiments on Nestling Recognition by Brown Noddies (Anous stolidus)

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Davies and Carrick (1962) suggested that adults should distinguish their own young from offspring of neighboring conspecifics by the time their young become mobile enough to leave the nest and mix with other young birds. The influence of the type of nest in shaping recognition behavior is illustrated by members of the family Laridae, which show diversity in nest sites and structure and in the age at which

chicks become active outside the nest. The young of ground-nesting Ring-billed Gulls (*Larus delawarensis;* Miller and Emlen 1975), Herring Gulls (*L. argentatus;* Tinbergen 1953), Sooty Terns (*Sterna fuscata;* Watson 1908), Crested Terns (*S. bergii;* Davies and Carrick 1962), and Royal Terns (*S. maxima;* Buckley and Buckley 1972) are all capable of moving away from the nest site within a few days after hatching, and adults are able to recognize their own offspring in these dense colonies early in the nestling period. Recognition of young by adults of the loosely colonial, marsh-nesting Franklin's Gull (*L. pipixcan*) begins after age 14 days, just before the age at which chicks begin to stray from their nests (Burger 1974). Cullen (1957) demonstrated that adult cliff-nesting Black-legged Kittiwakes (*Rissa tridactyla*), in which young fledge at about 5½ weeks of age, accept alien young on their isolated nesting ledges up to at least 4½ weeks posthatching. The White Tern (*Gygis alba*) will accept another nestling of any prefledging age in place of its own at its elevated nest site (Howell 1978).

Nest sites of the Brown Noddy (*Anous stolidus*) differ from colony to colony. On Ascension Island, the species is a cliff nester (Dorward and Ashmole 1963); in most of its Pacific colonies it is a ground nester (Murphy 1936); and at Dry Tortugas, Florida, it builds its nest in trees or bushes. This variety of nest sites allows a comparative study of the influence of the opportunity for nestlings to wander away from the nest on the onset of nestling recognition by adults.

I observed Brown Noddies during the 1979–1982 breeding seasons in a colony of approximately 15,000 adults on Bush Key, Dry Tortugas, Florida. In this colony, noddies lay one egg in an elevated nest constructed of vegetation, shells, and beach debris. Nests are placed in bay cedar (*Suriana maritima*), sea lavender (*Tournefortia gnaphalodes*), white mangrove (*Laguncularia racemosa*), and black mangrove (*Avicennia germinans*) and, less commonly, in or on several species of smaller plants. Ground nests are rare, and I found only two in my four seasons in the colony.

I removed individually banded, experimental nestlings (*n* = 56) of known ages from their natal nests and placed them in foreign nests from which resident nestlings were temporarily removed. As controls, I picked up and immediately replaced 14 nestlings in their own nests (sham-exchanged). I recorded the following behavioral responses of resident adults and displaced and control chicks for 1 h: adult broods, shades, feeds, preens, pecks chick; chick begs, initiates brooding by probing under adult, preens itself, leaves nest.

Experimental and control nestlings were of two classes: downy white and downy gray-brown, 1–6 days old; and brown-feathered, formerly either downy white or gray-brown, 15–20 days old. I made switches involving all combinations of these ages and colors (e.g. downy into feathered nest, opposite color) and used each nestling and nest only once.

I warmed or shaded nestlings temporarily removed from their natal nests during the periods of observation. Six nestlings were left in experimental nests as permanent exchanges. With Pesola scales, I weighed these nestlings on the day they were switched and on subsequent days. These measurements were compared with those of nestlings from 1979, 1980, and 1982, which were weighed in the same manner but not exchanged. I observed all experimental and control nests with binoculars from 8–12 m away, a distance sufficient to avoid disturbing the birds.

Brown Noddy nestlings of 1–4 days old are completely covered with down. At 6 days, the first sheaths (scapular) are visible. Six-day-old nestlings are able to walk around on the nest, but I never saw them leave it. Down color ranges from white through cream and gray-brown to dark brown, with lighter or darker tips on the crown, forehead, or wings. Body, wing, and tail feathers of nestlings of 15–20 days old are erupting. At 20 days, the mean length of the seventh primary is 33 mm (*n* = 41), and the plumage color begins to resemble closely that of adults. These nestlings have the white orbital half-ring, but the gray-brown neck color of the adult is absent, and natal down is still visible. These nestlings are capable of running rapidly when placed on the ground, and they are good climbers. Some jump from the nest when disturbed, some turn toward the intruder and call and strike with the bill, but most turn and face away from the intruder.

When nestlings were placed in foreign nests or sham-exchanged in control nests, adults in all control nests and in 51 of 56 experimental nests shaded or brooded them (Table 1). Adults at 58 experimental and control nests immediately returned to the nest after I placed the chick there, and adults of the other 12 returned within 1–2 min. Two nestlings that were neither brooded nor shaded were preened or fed by the resident adult. Only 3 experimental chicks did not receive any parental care during the hour, but only 1 of these 3 was pecked by the adult. Although adults pecked chicks in five experiments, only one pecking incident resulted in the departure of the chick from the nest for the remainder of the hour. In the other four nests, adults that initially pecked the nestlings eventually brooded them.

In all categories of exchanges, nestlings initiated begging, and some sought brooding (Table 2). Eight experimental nestlings preened themselves in the nests beside the resident adults. Although 6 feathered chicks hopped off the nest onto a nearby branch, 5 eventually returned to the nest: 3 were brooded, 1 was fed, and 1 begged and the adult attempted to brood it. The sixth remained on the edge of the nest. Although one chick that was pecked was neither brooded, fed, nor preened, it did not leave the nest and remained next to the adult.

All six of the nestlings not returned to their natal

TABLE 1. Responses of adult Brown Noddies to control nestlings and exchanged nestlings in their nests.

Experiment[a]	n	Brooded and/or shaded	Fed chick	Preened chick	Pecked chick
Downy control	9	9	1	0	0
Feathered control	5	5	0	1	0
D replaced DM	7	7	1	0	0
D replaced DO	7	7	2	0	0
F replaced F (O or M)	13	11	1[b]	1[b]	1[c]
D replaced F (O or M)	14	14	2	1	0
F replaced D (O or M)	15	12	0	2	4[d]

[a] F = feathered, 15–19 days old; D = downy, 1–6 days old; O = opposite color; M = same color.
[b] Not brooded or shaded.
[c] Eventually brooded.
[d] Three eventually brooded.

nests were permanently accepted by the resident adults. The gain in mass of each nestling subsequent to the day of permanent exchange was within or slightly above the range for nestlings that were not permanently exchanged.

Based on observations of a few nestlings, Lashley (1915) stated that Brown Noddies do not recognize their own young during the first days after hatching. Watson (1908) claimed that Brown Noddy nestlings leave the nest by age 20 days, and he proposed a functional recognition at this time. These reports are widely cited by students of individual recognition.

I found that by age 15 days, nestlings are left alone on the nest by the parents for varying lengths of time during the day, but the nestlings do not leave. In 44 regularly observed nests that fledged young in 1979 and 1980, only six nestlings moved outside the nest briefly before beginning to fly at ages of 40–48 days. Thus, although nestlings are capable of effective locomotion in branches and on the ground, they generally remain in the nest until they begin to fly. Watson's estimate of 20 days as the age of departure may have been based on such short-term movements by temporarily unattended younger nestlings.

Adult Brown Noddies did not discriminate against alien nestlings of both larger and smaller size that were placed in their nests, at least up to 20 days after the hatching of their own chick. In addition to accepting nestlings that differed in color from their own, Brown Noddies accepted alien chicks 9–16 days older or younger than their own offspring and therefore different in plumage. Older nestlings are more likely to appear in another bird's nest than are younger nestlings, and parents that have nestlings and are visited accidentally by awkward fliers might be able to compare two nestlings at once. This ability would not be detected in these switching experiments.

When young noddies begin to fly awkwardly, often landing on or near a neighbor's territory, the ability of adults to recognize their own young attains selective value. At this time adults do attack neighbors' fledglings, and they continue to feed only their own at their own nests. In 1979, fledglings returned to their nests regularly during the day and were fed there at least until 66 days old. I did not observe any adults feeding, brooding, or shading any fledglings other than their own. It is very difficult to determine exactly when recognition does occur in this species, because such information requires testing at a time when chicks are very mobile. Chicks 25–40 days old usually run when placed on their nests after handling, making this type of experiment impossible at later stages in the nestling period.

Among passerines, the association between timing

TABLE 2. Responses of Brown Noddy nestlings after being placed in foreign nests.

Experiment[a]	n	Begged or crawled under adult	Preened itself	Left nest
Downy control	9	2	0	0
Feathered control	5	2	2	0
D replaced DM	7	3	0	0
D replaced DO	7	4	0	0
F replaced F (O or M)	13	10	4	2[b]
D replaced F (O or M)	14	5	2	0
F replaced D (O or M)	15	9	2	4[c]

[a] F = feathered, 15–19 days old; D = downy, 1–6 days old; O = opposite color; M = same color.
[b] One eventually brooded.
[c] Three eventually brooded.

of nestling recognition and timing of mobility has been demonstrated in some species whose young do not mix with other broods before fledging: Barn Swallows and Tree Swallows (*Hirundo rustica* and *Tachycineta bicolor*; Burtt 1977), Bank Swallows (*Riparia riparia*; Beecher, Beecher, and Lumpkin 1981, Beecher, Beecher, and Hahn 1981), and Red-winged Blackbirds (*Agelaius phoeniceus*; Peek et al. 1972), all of which accept alien young in their nests until just before fledging.

Beecher, Beecher and Hahn (1981) suggested that, if alien nestlings can be distinguished from residents before fledging by their apparent differences in age, it may not be disadvantageous to delay recognition of a bird's own offspring until they become mobile away from the nest. Lashley (1915) also suggested that Sooty Terns can distinguish their own from younger nestlings by relative appearance alone, but he gave no evidence for this.

The degree of crowding of nests in a colony may also favor the early onset of nestling recognition by adults. Adult Mew Gulls (*Larus canus*; Pfeffer-Hulsemann 1955) and Royal Terns (Buckley and Buckley 1972), both of which nest in dense colonies on the ground, distinguish their own eggs from alien eggs placed in their nests. Although Common Murres (*Uria aalge*) and Black-legged Kittiwakes are both cliff nesters, murres' nests are tightly packed on ledges, and parents are able to recognize their own eggs (Tschanz 1959). Black-legged Kittiwakes, whose nesting ledges are generally not shared, do not seem to recognize their own nestlings before fledging. Gray Gulls (*L. modestus*), whose nest scrapes are 5–10 m apart (Howell et al. 1974), accept alien young in their nests but attack chicks, even their own, that are only a few centimeters outside the scrape. Von Rautenfeld (1978) found that cliff-nesting Herring Gulls accept chicks other than their own after 1 week of age, unlike the ground-nesting population observed by Tinbergen (1953).

Vegetation on oceanic islands varies with rainfall from year to year. Lashley and Watson may have observed nests of Brown Noddies at Dry Tortugas that may not have afforded vegetative protection to nestlings, and the nestlings they studied may have left nests to seek shade at an earlier age than did those in my 1979–1982 studies.

Early mixing of chicks is prevented at Dry Tortugas by noddies nesting in bushes instead of on the ground. If offspring are more mobile at an earlier age in ground-nesting colonies than at Dry Tortugas, one would expect an earlier onset of recognition of young by adults. The development of nestling recognition by Brown Noddies should be studied further in the different nesting situations observed in this species.

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A Case of Bigamy in the European Bee-eater (*Merops apiaster*)

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The European Bee-eater (*Merops apiaster*) is a 50-g colonial insectivorous bird. The usual course of events in our study area in the Camargue, France is that birds arrive in May and renovate or dig nest burrows. Males defend perches near their nests, at which "courtship" feeding takes place (Swift 1959, Avery et al. in prep.). During incubation, the eggs are rarely left unattended. Both sexes incubate by day (the male spends just over half this time on the nest), and at night the female roosts on the nest (Avery and Krebs unpubl. data). Both parents feed the young, and they are sometimes aided by another bird, which, at least sometimes, is a close relative (Dyer and Demeter 1981, Krebs and Avery unpubl. data). This note deals with a case of bigamy. Although only a single case, we think it is worth reporting, because bigamy is rare in species in which helpers occur (Wolfenden 1976) and the situation developed in an interesting way.

During the period of egg laying, our attention was drawn to two pairs (A and B) who occupied adjacent nest burrows (about 2 m apart). Both males were feeding and copulating with their own females. Over a period of 3 days, male A frequently attacked male B and eventually drove him from his nest site. We do not know what happened to male B, but we were able to follow the behavior of male A and his two females. Male A brought food to both females and mated with both of them during the period of egg laying (Table 1). Often both females would be outside their nest burrows at the same time, and male A frequently fed them both during these periods. On two occasions male A copulated with both females in the space of a minute. We saw no behaviors that would suggest that female B was unwilling to mate with male A, nor did we see any aggressive interactions between the females.

During incubation, female B received no help from

male A. She incubated the eggs alone and hatched all of them, even though the nest was left unattended for about 35% of the day-light hours. Male A was never seen to take food to nest B, which had the lowest feeding rate of nine nests that were watched. Female B's mean feeding rate was 1.1 visits/h, compared with 4.43 ± 0.45 (mean $\pm$ SE) visits/h for eight paired females at the same colony during the same time. Presumably because of this, the weight of nestlings in nest A (118 g) was greater than that of those in nest B (55 g). (The two nests began to hatch on the same day, and brood size was six in each case.) Both nests failed, as did many others, probably because of a period of bad weather.

Out of over 100 other nests we have watched, 2 have been attended by lone females during the nestling stage. We do not know whether or not these were bigamous females, although it is possible that they were.

This example of bigamy is interesting, because it does not fit with current hypotheses about the adaptive value of polygyny. Orians (1969) argued that females may sometimes gain by being the second female on a good territory rather than a lone female on a poor territory, and Pleszczynska (1978) was able to manipulate territory quality to produce polygyny. This is not the case here; female B already had access to the nest site when her mate was displaced. Alatalo et al. (1981) suggested that male Pied Flycatchers (*Ficedula hypoleuca*) could "trick" females into mating with them by setting up new territories while their

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TABLE 1. The behavior of male A toward the two females and their nests.

Behavior	Frequency	
	Nest A	Nest B
Copulations	6	7
Feeding of female (visits)	72	11
Feeding of nestlings (visits)	45	0