

PROLONGED PARENTAL CARE IN ROYAL TERNS AND OTHER BIRDS

N. PHILIP ASHMOLE AND HUMBERTO TOVAR S.

DURING the last thirty years ornithologists have accumulated a vast body of quantitative information on many aspects of the breeding biology of a large variety of bird species, but adequate information on the weeks following departure of the young birds from the nest is available for only a handful of species. As this period includes the critical time when the young become independent of their parents—and one when they suffer heavy mortality—the seriousness of this gap in present knowledge is obvious. The gap exists because of the difficulties of obtaining data after young birds have left the nest. For most species intensive efforts are necessary to overcome these difficulties. Our interest in the postfledging period was stimulated by a chance observation that led us to consider the selective pressures determining the length of the period of dependence of young birds.

OBSERVATIONS

We watched groups of Royal Terns (*Thalasseus maximus*) and Elegant Terns (*Thalasseus elegans*) at Laguna Grande, Departamento de Ica, Peru, on several occasions between early December 1966 and early January 1967. The Elegant Tern winters in considerable numbers on the Peruvian coast, but the Royal Tern is seen less often. However, a group of Royal Terns is regularly present during the northern winter, and odd birds stay during the northern summer at Laguna Grande, which at 14° S may be the southernmost wintering station for the species on the west coast of South America (cf. Koepcke, 1964). At the time of our visits on 5, 6, and 10 December 1966 more than 1,000 Elegant Terns and at least 100 Royal Terns were present at Laguna Grande; on 11 January 1967 about 300 Royal Terns were present.

Most of the Royal Terns were adults in the middle of the annual molt of their remiges, but perhaps one tenth were first winter birds (i.e., about 6 months old), distinguishable in flight by their worn, and therefore blackish, primaries, and when perched by the darker scapulars and inner secondaries. At least four of the Royal Terns had bands, and of these one adult and one first winter bird were shot 10 December 1966 to determine their place of origin. The adult, a female, proved to have been banded as a juvenile by Lovett Williams near Pascagoula, Mississippi in July 1964. The young bird, also a female, was banded as a juvenile by H. T. Davis on Wainwright Island, Pamlico Sound, North Carolina, 4 July 1966, and

was thus probably a little less than 6 months old when collected. In each wing the innermost two juvenal primaries and the innermost five secondaries (numbers 20 through 24) had been replaced by new feathers. No remiges were in the process of growth, and "discontinuities" (Ashmole, 1963*b*) were noticeable between the old and new feathers; probably the molt had started in the northern hemisphere and then stopped during the southward migration. (In some young birds none of the juvenal primaries had yet been replaced.) In the tail the two innermost pairs of juvenal rectrices had been replaced and the vanes of the new third pair were just breaking their sheaths. Some growing body feathers were present on the head, mantle, and dorsal surface of the wings.

On the first day we watched this group of Royal Terns, we several times heard individuals utter a series of loud calls in flight, and noted that these birds were always carrying fish. Twice we saw the fish given to another bird, but could not determine the age of the recipient. As behavior of this kind is used by adult *Thalasseus* terns during courtship as well as when feeding young, it was clearly important to determine whether we were witnessing premature or residual courtship behavior or prolonged parental care. On 10 December we returned to the area and watched from 0545 until 0930, using a telescope as well as binoculars, and three times saw adults give fish to young birds. The first observation was of an adult fishing, with a young bird flying below and behind it and persistently using the squeaky begging call. Eventually the adult caught a fish and then flew some distance away from the main group of birds, followed by the begging juvenile that then settled on the water. The adult flew down and gave it the fish without itself settling; we could not see whether the fish was actually passed from bill to bill or dropped to the young bird from just above its head. The young bird continued begging for at least 10 minutes, partly in flight below a fishing adult (perhaps the one that had fed it), but later also on the ground, when the begging was apparently directed towards a flying bird or birds.

A little later an adult with a fish flew in past the resting group, calling persistently. It was soon joined by a young bird, which followed it for a minute or more as it flew away from the main group. The adult then dropped the fish—evidently deliberately for it made no effort to retrieve it as these birds normally do—and the young bird picked it up from the water surface. Later this juvenile was seen hunting by itself, though it was not seen to catch anything. The third observation was of a calling adult that flew in with a fish, was joined by a young bird, and was also pursued for a short time by another adult. The adult with the fish and the young bird then flew out to sea, the young bird settled, and the adult hovered and gave it the fish. The young bird in this case was probably

a banded individual. The same day we watched an adult fly in with a fish and circle four times around the various groups of perched birds, calling about every 2 seconds over a period of some 5 minutes, but it only succeeded in attracting the attention of a Band-tailed Gull (*Larus belcheri*) which pursued it vigorously. Eventually the adult tern swallowed the fish itself.

Adults were again seen feeding young (by H. T. S.) at Laguna Grande on 11 January 1967. Subsequently small groups of Royal Terns were watched (by H. T. S.) at Lagunilla, a bay a few miles north of Laguna Grande, on 13 March, 31 March, 7 April, and 21 April 1967, but juveniles were not heard begging for food, nor were adults seen feeding them. On 13 March juveniles were seen successfully fishing for themselves.

We have described our observations in some detail because they indicate that adult Royal Terns sometimes continue to feed their young until they are about 7 months old and have been able to fly for more than 5 months. Although we have no proof that the adults feed only their own young, the persistent calling by both adults and young strongly suggests that individual recognition is involved.

Adult feeding of young after fledging has previously been reported in at least two other members of the genus *Thalasseus*. After observing Elegant Terns in San Diego Bay, California during the summer and fall seasons of 1953, 1954, and 1955, Monroe (1956) says "Immatures continue begging for food, and have been noted doing so into late November. Begging is accomplished exactly as in the Royal Tern. The immature bird, upon arrival of an adult with food, lowers its head, thereby erecting the crest feathers, chases the adult with head low and slightly uptilted, and peeps continuously until fed." As only small numbers of Elegant Terns were present in San Diego Bay later than October (the area being visited by the species mainly in the late summer and early fall) the fact that Monroe did not record begging later may merely reflect the absence of birds. However we did not observe any begging among the wintering Elegant Terns in Peru in December or any birds arriving at the resting area carrying fish. In contrast the feeding behavior by Royal Terns was conspicuous, despite the smaller numbers of this species.

Adult Elegant Terns feeding young in California were also observed by Pyle and Small (1951) in August 1951. Among other members of the genus, we are aware of relevant data only for the Sandwich Tern (*Thalasseus sandvicensis*); Tinbergen (1953: 229) watched adults feeding chicks during migration in August, and David Lack (pers. comm.) saw adults of this species feeding young in Norfolk, England, at least 20 miles from their breeding colony. Similar behavior certainly occurs in a number of other terns and gulls, but seems not to have been studied systematically. Palmer

(1941: 103) in his study of the Common Tern (*Sterna hirundo*) records that "As some juvenals are still being fed by their parents during migration, the begging note is often heard in traveling flocks. Not all juvenals do this, for some flocks, reported by various writers, were apparently composed entirely of young birds." Ralph W. Schreiber informed us (orally) that he regularly observed young Herring Gulls (*Larus argentatus*) being fed by adults—under circumstances strongly suggesting that they were the parents—on rubbish dumps in Maine from August to October; some of the gulls involved were banded in colonies several hundred miles away. Similarly David Lack (pers. comm.) has observed young Herring Gulls repeatedly begging their (presumed) parents for food in Cornwall, England at the end of October.

Thus evidence suggests that parental care persists after departure from the breeding area in a number of larids. However the feeding of young Royal Terns, apparently by their own parents, more than 5 months after fledging and after a trans-equatorial migration of at least 3,000 miles, seems to have no recorded parallel in other species. The closest analogy may be with the geese in which family parties persist through the southward migration, the following winter, and even the return migration to the breeding grounds (see Hochbaum, 1955: 93).

DISCUSSION

In view of the high mortality suffered by young birds of a wide variety of species shortly after they learn to fly, which certainly results largely from their relative inefficiency in obtaining food, it is perhaps surprising that more species do not continue feeding their fledged young over an extended period. The difficulty of maintaining contact between parents and their young, especially in species that show a postbreeding dispersal from the nesting area, probably constitutes a serious barrier to the evolution of prolonged postfledging parental care in many species. Royal Terns share with other members of the genus *Thalasseus* a number of ecological characteristics that may have been important preadaptations. First as the young wander from the nest site at an early age, this species doubtless evolved, like some other larids, mechanisms for individual recognition between parents and young chicks (Davies and Carrick, 1962), probably largely by variation among individual calls; such recognition could readily persist after fledging. Second the birds tend to roost at night and to rest during the day, both on migration and in winter quarters, in compact flocks close to where they obtain their food; this must greatly facilitate the maintenance of contact among the members of a family. Third they catch prey of a substantial size which can be easily and quickly transferred to the young.

Similar reasoning is used by Nelson (1966*b*) to explain the fact that the young of tropical boobies (*Sula* spp.) are fed by their parents near the nest site for a long time after they can fly (and apparently sometimes until they are nearly a year old—Verner, 1961), while young Gannets (*Sula bassana*), which go to sea even before they can fly, are not fed after they leave the breeding colony. Nelson believes that it would be impracticable for adult Gannets to maintain contact with their own young once the young leave the immediate vicinity of the colony. Among resident species, on the other hand, the maintenance of contact between parents and offspring should not present an insuperable obstacle to the evolution of prolonged parental care, but feeding young for more than a few weeks after fledging appears to be uncommon among birds. This implies that in most species the young soon become sufficiently expert at finding food for themselves, and that any selective advantage gained by parents continuing to feed their young is outweighed by the disadvantageous diversion of energy resources of the adults from other important functions, especially the raising of second broods or the replacement of feathers (cf. Pitelka, 1958). On the other hand in those species that need a high degree of skill for hunting success and whose young require a considerable time to perfect their skill, prolonged parental care is essential and may prevent any attempt to raise a second brood if the first is successful.

The raising of a large brood implies that the parents can easily obtain large quantities of food in the breeding season. Thus in species that lay large clutches even inexperienced juveniles may generally have little difficulty in obtaining the much smaller quantities of food they need to maintain themselves in the time just after fledging, so one might predict that prolonged parental care would not often occur in species with large clutch sizes. On the other hand low clutch size, and especially the minimum clutch of one, implies scarcity of food or strong competition for it (Ashmole, 1963*a*, Amadon, 1964), so prolonged parental care should be especially common among birds that have small clutches and also use specialized feeding methods which can be perfected only by a prolonged learning process. The most critical situation will be in those species that capture relatively large prey at infrequent intervals, because in these birds even a few successive missed opportunities by an inexperienced bird could have fatal results.

Although we have not attempted a comprehensive review, the literature provides some support for the prediction that those birds whose methods of obtaining food require great skill should have a considerable period of post-fledging parental feeding of the young, and should often lay small clutches and be single-brooded.

Perhaps the most spectacular example is that of the Crowned Eagle

(*Stephanoaetus coronatus*), studied by Brown (1966), which feeds mainly on agile prey such as small antelopes, hyrax, and monkeys. In this species the young eagle is fed, almost always at the nest, for as long as 11.5 months after the time of fledging, until it is about 15 months old. However it sometimes kills for itself long before it becomes independent, apparently when it has not been fed by the parents for several days. As might be expected, Crowned Eagles breed only in alternate years, as the female at least is involved in breeding activities for a total of 17–18 months. This species provides an excellent example of a bird eating large, relatively scarce prey, in which even the adults may sometimes have difficulty in making kills often enough, as suggested by failure to breed in a year when the normal prey were less abundant than usual.

The observations of Fowler and Cope (1964) on the Harpy Eagle (*Harpia harpyja*) in British Guiana show that the breeding biology of this species is similar to that of the Crowned Eagle. A juvenile 10 months old was still being fed by an adult and showed no signs of hunting for itself, although replacement of the juvenal rectrices and primaries had already started at the age of about 8 months. In most members of the Accipitridae the period of parental care after the young leave the nest is much shorter, but it amounts to several months in some other large species (see Brown, 1952–53; 1955).

The Falconidae normally raise only one brood per year and the parents feed the young for several weeks after fledging (see Cade, 1960). The same is true for some owls. The Tawny Owl (*Strix aluco*) which eats mainly small rodents (Southern, 1954) is single-brooded, and in Britain the clutch is small and the young are dependent on their parents for food in the 2½ to 3 months after fledging; nevertheless many young die of starvation after the adults stop feeding them (Southern *et al.*, 1954). During the dependent period the young learn the way about the territory of their parents, but have not been seen practicing hunting; the behavior of the young during the last few weeks before they become independent is so difficult to observe that there are few relevant observations. This example thus supports the hypothesis outlined above only if it can be assumed that the young birds are acquiring skills or knowledge in the postfledging dependent period that will make them more efficient when they have to hunt for themselves. Southern's (1954) discussion of the situation in other owls shows that some species (Barn Owl, *Tyto alba*, and Short-eared Owl, *Asio flammeus*), which must be regarded as equally skilled in hunting, contrast with the Tawny Owl in having relatively short periods of parental care and raising several broods in seasons when prey is very abundant.

Among fish-eating birds the kingfishers are clearly relevant to this discussion. Although we have not seen a detailed account of the postfledging

period of any species, the description by Bralliar (in Bent, 1940: 117) of how young Belted Kingfishers (*Megaceryle alcyon*) are taught to fish by their parents suggests the way in which members of this group achieve the transition to independence. According to Bralliar the learning period in this species lasts only a week or so, but it presumably varies between species according to the abundance of prey at the critical time. In the Green Kingfisher (*Chloroceryle americana*) Skutch (in Bent, 1940: 144) describes how a young bird that had been out of the nest for 29 days begged for a fish from its father, but was chased away. Young of the Kingfisher (*Alcedo atthis*) apparently become independent fairly soon after fledging. This species is one of the few birds in which successive broods sometimes overlap substantially, so that the male may be simultaneously involved in feeding young at one nest and incubating at another (Brown, 1934; Swanberg, 1952). This fact and also the high clutch size (generally 6-7) suggest that, like some owls when rodents are very abundant, both adults and young of this species of kingfisher can obtain food easily during the breeding season, in spite of their specialized method of feeding.

The frigate-birds (Fregatidae) are another group in which the acquisition of food requires great skill, but their food is often scarce. In the Ascension Island Frigate-bird (*Fregata aquila*) the chicks begin to fly during their 6th or 7th month, but remain at least partly dependent on their parents for a further 3 or 4 months. Stonehouse and Stonehouse (1963), who studied the species, suggest that "the long period of partial dependence may help the young birds to attain proficiency in accurate flying, a necessary skill in a species which obtains much of its food either in the air, or by skimming over the sea or ground and taking food without settling." Nelson (1966a), studying the Great Frigate-bird (*Fregata minor*) on Tower Island in the Galápagos, found that the young birds were dependent on their parents for 6 months after fledging, and that a successful breeding cycle took more than a year; apparently these birds, like the Crowned Eagle, can breed successfully only in alternate years. Nelson found that in spite of the prolonged postfledging feeding several young died of starvation about when they were becoming independent. This example demonstrates particularly well the difficulty of the transition to independence in species whose food is sometimes scarce and whose feeding methods are highly skilled.

Members of several of the groups discussed above have been observed performing "play" activities of a kind that must aid in the acquisition of hunting skill. Stonehouse and Stonehouse (1963) report juvenile Ascension Island Frigate-birds in small groups over the coast "flying together, catching feathers and strands of sea-weed from each other in mid-air, and attacking incoming boobies." Similarly Gibson-Hill (1947) says of

Fregata minor "They seem, in fact, to be much addicted to picking things up, and small groups of birds of various ages often play follow-my-leader over a rock-pool, each in turn swooping down over the water and pausing just above its surface. They also take a great delight in pulling up pieces of dead creeper, and in trying to break prominent branches off low trees." Swanberg (1952) records a young Kingfisher probably 50 days old "several times diving for and fetching a twig, 1.5 cm long, floating along in the water." Among the birds of prey there are a number of records of comparable behavior. L. Tinbergen (quoted by Thorpe, 1963: 362) watched young Kestrels (*Falco tinnunculus*) playfully hunting a variety of inanimate objects, although they were already able to hunt successfully for themselves, while Munro (1954) observed a Prairie Falcon (*Falco mexicanus*) of unspecified age repeatedly dropping or tossing, and then catching, pieces of dried cow manure.

After submitting this article we had an opportunity to observe young Inca Terns (*Larosterna inca*) practicing hunting around Isla Chincha Sur, Peru. For several hours on 15, 16, and 17 August 1967 we watched about 20 juveniles which had recently learned to fly (certainly in the previous month) and which probably averaged about 2 months old. From time to time one of these birds would leave the rock on which it was perched, circle low over the water and then "plunge to surface" and pick up an inanimate object in the water; the birds also sometimes used "contact dipping." (In "plunging to surface" the bird drops to the surface but does not submerge completely, while in "contact dipping" forward flight does not stop and usually only the bill touches the water: see Ashmole and Ashmole, 1967.) The objects picked up were mainly pieces of algae between about 1 and 10 cm long. After obtaining one of these, and sometimes mandibulating it, the bird would fly a short distance (between about 1 and 50 m), drop it, and then frequently retrieve it. This procedure was repeated persistently, in one case at least ten times with the same object. This kind of behavior in one juvenile often attracted others, which either competed for the same object or picked up different ones. Occasionally a bird showed another type of behavior, flying low and fast and executing rapid twists and turns without touching the surface. Unlike the plunging and dipping movements, which were generally or always triggered by the sight of an object in the water, these aerobatics were apparently not dependent on any specific external stimulus, but occurred spontaneously.

The hunting practice occurred at all times of day—perhaps especially in the early morning—but it was very intermittent; there were often periods of as much as half an hour when all the juveniles were resting, followed by a short burst of activity. To give an idea of the intensity this activity could

reach, in the 16 minutes between the time we noticed that one of the juveniles was recognizable by a gap in one wing and the time we lost it round a corner of the island, this individual made 8 separate sorties from its base on an offshore rock, and in the course of these made 40 to 50 contacts with the water. The great majority of these contacts were plunges to surface to retrieve objects, but a few were followed by bathing behavior. Adult Inca Terns plunge to surface in a similar way when they start bathing as well as while hunting, but we have never seen them picking up inedible objects.

During our observations we often saw the juveniles beg for fish from adults, and feeding was several times observed. So far as we could tell the juveniles at this age do not go out to sea and fish, but spend a considerable proportion of their time and energy developing their hunting skills. Plunging to surface and contact dipping are the two normal feeding methods of the species, and both must be executed with great speed and skill if they are to be successful. The value of practicing them before independence is self-evident.

We hope this brief discussion may serve to emphasize the need for more information about the critical period when young birds are learning to catch prey for themselves. In particular it would be of great interest to have for a number of species quantitative data on the proportion of prey supplied by the parents, and the proportion caught by the young bird at different stages during the postfledging period. Another possible approach is exemplified by observations N. P. A. made on Ascension Island in 1958, where Ascension Island Frigate-birds frequently preyed on small chicks of Sooty Terns (*Sterna fuscata*). The frigate-birds would patrol over the tern colonies, swooping at intervals to try to pick up exposed chicks without alighting. Casual observations suggested that adults were more often successful at this than white-headed juveniles, so a tern colony was watched for the whole of two days, 22 and 28 February 1958. During the first day adults obtained 25 chicks in 89 attempts, while juveniles obtained 6 chicks in 44 attempts. On the second day adults took 32 chicks in 129 attempts, but juveniles made only 9 classifiable attempts, of which 2 were successful. These data suggest that the adults were more efficient than juveniles in the use of this hunting technique, but the difference is nonsignificant. It was not possible to collect further data on this species, but we hope to investigate the acquisition of hunting skill in terns by making similar observations on them in the future.

ACKNOWLEDGMENTS

Field work on Peruvian sea birds was supported by NSF grant GB-3983 to N. P. A., while H. Laurence Achilles also gave vital assistance. Rómulo Jordán, David Lack, and Charles G. Sibley kindly read and criticized the manuscript.

SUMMARY

During December 1966 and January 1967 adult Royal Terns wintering on the coast of Peru were seen to feed juveniles hatched about six months previously in North America. Feeding of young by parents after departure from the breeding grounds has been recorded in other members of the genus *Thalasseus* and in other Laridae, but the age of the young and the distance traveled make this case unusual. Some instances of prolonged parental care in other groups are briefly reviewed; its occurrence appears to be correlated with the use of highly skilled feeding methods and the exploitation of scarce foods, and thus with low clutch size. Species showing it do not normally have second broods. Juveniles of species exploiting active prey animals difficult to catch often show "play" activities related to the acquisition of hunting skill. More information is needed about the critical period of transition to independence in young birds.

LITERATURE CITED

- AMADON, D. 1964. The evolution of low reproductive rates in birds. *Evolution*, **18**: 105-110.
- ASHMOLE, N. P. 1963a. The regulation of numbers of tropical oceanic birds. *Ibis*, **103b**: 458-473.
- ASHMOLE, N. P. 1963b. Molt and breeding in populations of the Sooty Tern *Sterna fuscata*. *Postilla* (Yale Univ.), no. 76: 1-18.
- ASHMOLE, N. P., AND M. J. ASHMOLE. 1967. Comparative feeding ecology of sea birds of a tropical oceanic island. *Peabody Mus. Nat. Hist., Yale Univ., Bull.* 24.
- BENT, A. C. 1940. Life histories of North American cuckoos, goatsuckers, humming-birds and their allies. *U. S. Nat. Mus., Bull.* 176.
- BROWN, L. H. 1952-53. On the biology of the large birds of prey of the Embu district, Kenya Colony. *Ibis*, **94**: 577-620; **95**: 74-114.
- BROWN, L. H. 1955. Supplementary notes on the biology of the large birds of prey of Embu district, Kenya Colony. *Ibis*, **97**: 38-64, 183-221.
- BROWN, L. H. 1966. Observations on some Kenya eagles. *Ibis*, **108**: 531-572.
- BROWN, R. L. 1934. Some breeding-habits of Kingfishers. *Brit. Birds*, **28**: 83-84.
- CADE, T. J. 1960. Ecology of the peregrine and gyrfalcon populations in Alaska. *Univ. Calif. Publ. Zoöl.*, **63**(3): 151-290.
- DAVIES, S. J. J. F., AND R. CARRICK. 1962. On the ability of Crested Terns, *Sterna bergii*, to recognize their own chicks. *Austral. J. Zool.*, **10**: 171-177.
- FOWLER, J. M., AND J. B. COPE. 1964. Notes on the Harpy Eagle in British Guiana. *Auk*, **81**: 257-273.
- GIBSON-HILL, C. A. 1947. Notes on the birds of Christmas Island. *Raffles Mus., Singapore, Bull.*, **18**: 87-165.
- HOCHBAUM, H. A. 1955. *Travels and traditions of waterfowl*. Minneapolis, Univ. Minnesota Press.
- KOEFCKE, M. 1964. *Las Aves del Departamento de Lima*. Lima, published by the author.
- MONROE, B. L., JR. 1956. Observations of Elegant Terns at San Diego, California. *Wilson Bull.*, **68**: 239-244.
- MUNRO, D. A. 1954. Prairie Falcon "playing." *Auk*, **71**: 333-334.

- NELSON, J. B. 1966a. The Man-o'-War Bird. *Natural History*, **75**(5): 32-39.
- NELSON, J. B. 1966b. The breeding biology of the Gannet *Sula bassana* on the Bass Rock, Scotland. *Ibis*, **108**: 584-626.
- PALMER, R. S. 1941. A behavior study of the Common Tern (*Sterna hirundo hirundo* L.). *Proc. Boston Soc. Nat. Hist.*, **42**(1).
- PITELKA, F. A. 1958. Timing of molt in Steller Jays of the Queen Charlotte Islands, British Columbia. *Condor*, **60**: 38-49.
- PYLE, R. L., AND A. SMALL. 1951. Southern Pacific Coast Region. *Audubon Field Notes*, **5**: 307-309.
- SOUTHERN, H. N. 1954. Tawny Owls and their prey. *Ibis*, **96**: 384-410.
- SOUTHERN, H. N., R. VAUGHAN, AND R. C. MUIR. 1954. The behaviour of young Tawny Owls after fledging. *Bird Study*, **1**: 101-110.
- STONEHOUSE, B., AND S. STONEHOUSE. 1963. The Frigate Bird *Fregata aquila* of Ascension Island. *Ibis*, **103b**: 409-422.
- SWANBERG, P. O. 1952. Observations on feeding, brooding and bathing habits in a pair of Kingfishers (*Alcedo atthis*) [in Swedish, English summary]. *Vår. Fågelvärld*, **11**: 49-66.
- THORPE, W. H. 1963. *Learning and instinct in animals*. 2nd ed. London, Methuen.
- TINBERGEN, N. 1953. *The Herring Gull's world*. London, Collins.
- VERNER, J. 1961. Nesting activities of the Red-footed Booby in British Honduras. *Auk*, **78**: 573-594.

Department of Biology and Peabody Museum of Natural History, Yale University, New Haven, Conn., and Instituto del Mar del Perú, Callao, Lima, Peru.