

## MATE REPLACEMENT IN PURPLE MARTINS: LITTLE EVIDENCE FOR ALTRUISM

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In a somewhat controversial study, Power (1975) attempted to provide evidence against altruism in Mountain Bluebirds (*Sialia currucoides*). After removing males, he found that their replacements did not aid the missing males' mates with defense or feeding of the young (see Emlen 1976, Konecni and Power 1976). A similar approach was used by Pierotti (1980) with Western Gulls (*Larus occidentalis*) and by Weatherhead and Robertson (1980) with Savannah Sparrows (*Passerculus sandwichensis*). My purpose here is to report comparable data for Purple Martins (*Progne subis*), based on a 13-year investigation.

My study differs from the previous ones in that I performed no removal experiments. My data resulted from cases in which members of mated pairs disappeared, presumably owing to natural causes; thus, they also provide information on the frequency of mate loss under natural conditions. My observations were conducted in northern Texas at one colony-site from 1968 to 1976 and at another from 1977 to 1979 and in 1981. Details on study areas and how individual martins were recognized are given elsewhere (Brown 1979, 1980). Purple Martins at my study sites nested entirely in manmade apartment houses.

After Purple Martins form pairs and lay their eggs, one member of a mated pair occasionally disappears. Of 241 pairs present at my study colonies, 9 males (3.7%) and 2 females (0.8%) were lost, leaving widows or widowers, from egg-laying through feeding of young. These figures do not include mate losses and replacements prior to egg-laying, or cases in which both members of a pair abandoned the nest simultaneously (e.g., as when evicted by Starlings, *Sturnus vulgaris*, and House Sparrows, *Passer domesticus*). These figures show that adult martins rarely disappeared at these colonies and that pairs were stable throughout the eggs-to-fledging period.

Of the nine males lost, eight disappeared, and the ninth was scored as a loss because he abandoned a female, although he remained in the colony with another female (see below). Seven of these males were feeding young when they disappeared; the smallest nestlings who lost their fathers were 11 days old, the oldest 20 days. None of these seven males was replaced, although in six cases other unmated males took up residence elsewhere in the colony after the losses of these males. Other males showed no sustained interest in the nests of the lost males, although visiting males frequently peered into the nests for short periods. The widowed females continued to feed their nestlings and in all cases successfully fledged some of them. The two remaining lost males were replaced, as described below.

On 2-5 May 1974, a yearling male (M1) formed pair-bonds with two females (F1 and F2). (Polygyny is rare although regular in Purple Martins; see Brown 1975, 1979.) The females claimed, and later nested in, adjacent holes. These two holes were the only ones defended by M1. He escorted both females, defended both, and slept (and presumably copulated; see Brown 1980) with both. Another yearling male (M2) arrived on 11 May and claimed a hole adjacent to that of F2. He attempted to court F2, but M1 defended her. She also was hostile to M2 and would not allow him to approach her nest. On 21 May both females

laid their first eggs. On that date M1 abruptly abandoned F2 and no longer defended her, confining his attention to F1. However, F2 remained hostile toward M2 until 23 May, when she apparently accepted him and allowed him to enter her nest. She completed her clutch of four eggs on 24 May and began incubating. Although M2 had gone through no true courtship or nest-building period with F2, it is possible that he sired one or two of her young, inasmuch as F2 was tolerant of him during her egg-laying period. Allen and Nice (1952) reported that Purple Martins cease copulation with the laying of the first egg, but they presented no data on which to base this assertion. M2 began guarding F2's nest during incubation as would a normal male. He later fed the young, removed feces, and harassed potential predators (i.e., sparrows and people) that approached. Four young successfully fledged on 5-6 July. M1 and F1 also fledged four young. In summary, F2 essentially lost her mate during egg-laying, and M2 served as a replacement and perhaps sired part of her brood.

The second case of mate replacement occurred in 1981. On 25 May I observed that the adult male mate of an incubating female was absent. He may have disappeared one or two days beforehand. On 25 May a yearling male was courting the incubating female and apparently was trying to establish a pair-bond with her. She, however, seemed hostile toward him and did not allow him in her nest until 29 May. At that time she apparently accepted him and allowed him to enter her nest. He began guarding the nest whenever she left. When three of her eggs hatched on 3 June, the male assisted her in feeding the young, removing feces, and in harassing humans near the nest. The young successfully fledged on 1-2 July. Thus, this male clearly aided in rearing young that could not have been his own.

Both females who disappeared during my study were in early stages of incubation. By the time I determined with certainty that they were gone, both widowed males were already courting new females who appeared in the colony. Each (both were adults) had attracted and established a pair-bond with a replacement two to four days after the loss of his first mate. The replacement females seemed to ignore the previous females' clutches and built nests over them, in which they laid their own eggs.

As in Power's (1975) study, I found little evidence for altruism in Purple Martins. Although both females who disappeared after laying eggs were replaced, the replacements were definitely not parental toward the previous females' eggs. Seven of nine males (77.8%) who disappeared were not replaced by any males, although unmated males were available in the colony and presumably could have moved into the vacated males' territories. Of the two replacement males present, one may have sired one or two of the brood members, so his behavior may have been selfish. The remaining replacement male undoubtedly did not sire the young he fed because the eggs in question were laid before he arrived in the colony. I regard his behavior as anomalous because none of the generally accepted reasons for helping (e.g., enhanced predator avoidance, chance for future breeding, etc.) seems to apply in Purple Martins.

The very low incidence of natural mate loss in Purple Martins reported here suggests that the behavior of replacements is probably a minor point, because replacements may have little overall selective importance due to their rarity. The same may be true for Mountain Bluebirds (Power 1975), Western Gulls (Pierotti 1980), and Savannah Sparrows (Weatherhead and Robertson 1980), inasmuch as the frequency of mate loss under natural conditions is not known for these species.

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## WATER LOSS FROM PIPPED WEDGE-TAILED SHEARWATER EGGS

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**ABSTRACT.**—The sequence of events during the prolonged pipping process in the Wedge-tailed Shearwater (*Puffinus pacificus*) was chronicled. The initial event, a series of star-fractures in the shell, occurred five to six days before the chick hatched. The daily rate of water loss from pipped eggs was considerably greater than that from un-pipped eggs; the highest water loss (858.4 mg/day) occurred in eggs with a distinct pip-hole. It was estimated that approximately 16% of the water loss from eggs with a pip-hole could be attributed to embryonic pulmonary ventilation. Comparison with three other species of procellariiform sea birds with a seven-fold range of egg mass, revealed that the total water loss from the egg over the entire incubation period varied from 16.1 to 18.6% of the fresh egg mass. The main difference between the four species lay in the way in which the water loss was divided between the pre-pipping period and the period between the initiation of pipping and hatching.

The initial event in the pipping process of the eggs of many species of birds is the penetration, by the embryo's beak, of the air cell at the blunt pole of the egg, an event that has been termed "internal pipping" (Ar et al. 1980). Internal pipping allows the embryo to rebreathe the air in the aircell but it has little effect on the water loss from the egg, because the integrity of the egg shell, which presents the main barrier to the diffusion of water vapor out of the egg (Paganelli 1980), is intact. Following internal pipping, a series of star-fractures is made in the shell, by the embryo, and, subsequently, a distinct hole—the "pip-hole"—is made in the shell. Both of these events are likely to result in an increased rate of water loss from the egg (Whittow 1980), because the water loss is then no longer limited by the number and size of the minute pores in the shell, through which gases diffuse.

In the eggs of the Wedge-tailed Shearwater (*Puffinus pacificus*) the sequence of events during pipping differs markedly from that just described. In this species, the initial event in the pipping process is a series of star-fractures in the shell (Ackerman et al. 1980), an event that we have called "external pipping" (Grant et al. 1982a). In addition, the duration of the pipping process—from the

initial star-fractures in the shell, to the hatching of the chick—is relatively long (Ackerman et al. 1980, Whittow 1980). It seemed likely, therefore, that a substantial fraction of the total water loss from the egg of the Wedge-tailed Shearwater might occur during the pipped phase of incubation. We conducted a study to document the sequence of events during pipping and to measure directly the water loss during the pip-to-hatch period. An ancillary objective was to estimate the contribution of embryonic pulmonary ventilation to the water loss during this period.

### PROCEDURES AND METHODS

Observations in the field were made on Manana Island, a small island off the main island of Oahu, Hawaii. Eggs of known age were carefully examined on alternate days in late July and August 1979, in order to chronicle the events during pipping in naturally-incubated eggs. Internally-pipped eggs were identified by "peeping" and/or breathing sounds made by the chick, aided by auscultation with a bell stethoscope. The mass loss of externally-pipped eggs was also measured on Manana; the eggs were weighed to 0.01 g at intervals of 46.9-72.6 h on an Ohaus balance (model 1010-10).

Other shearwater eggs were collected and incubated in the laboratory at 36°C (relative humidity 40%). The eggs were four to five weeks old when first placed in the incubator; the eggs were turned twice daily before external pipping. The artificially incubated eggs were weighed periodically to measure the pre-pipping daily water loss (Ackerman et al. 1980). After the initial star-fracture of the shell had occurred, the eggs were weighed daily.

The respiratory water loss ( $\dot{m}_{\text{H}_2\text{O}}$ , g/h) from the embryo after internal pipping was calculated from the following equation:

$$\dot{m}_{\text{H}_2\text{O}} = \dot{V}_E (e_{\text{ex}} - \theta e_{\text{in}})$$

$\dot{V}_E$  = mean pulmonary ventilation (l/h) reported for the shearwater's embryo (Pettit and Whittow 1982)  
 $e_{\text{ex}}$  = water vapor content of expired air (g/l) derived from

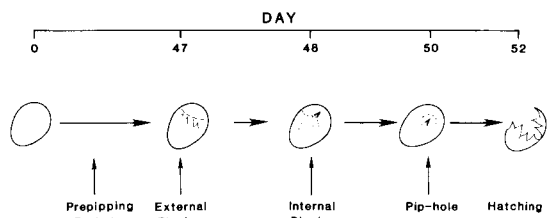


FIGURE 1. Sequence of events during the pipping process in the egg of Wedge-tailed Shearwater.