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ON THE BEHAVIOR OF THE BLACK SWIFT¹

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Abstract. The behavior of Black Swifts was studied in southern California from 1990 to 1992. Four types of aerial interactions were distinguished: (a) group chase, (b) pair chase, (c) pair contact, and (d) touch and grasp. The latter two interactions can be intraspecific or interspecific. Aerial copulation was not observed. Nestlings, from age 18 days onward, and adults gave hostile or deterrence displays by wing-raising. Begging by nestlings was silent but aggressive toward the adult. Silent begging may be an antipredator strategy for a species that produces a single chick per season. Nestlings have a far more conspicuous white facial marking than adults; this may function as a target signal to guide food delivery in the dimly lit nesting conditions and as an aid for the adult to find the nest when arriving late at night. Adults roosted on the nest for the first half of the nestling period and

then most roosted on the cave walls. During incubation and early brooding, an adult always remained at the nest, and food transfer between adults was observed during this period.

Key words: behavior, aerial and hostile displays, begging, roosting, *Cypseloides niger*.

Swifts as a group are remarkably uniform in shape, which makes them difficult to identify, and their aerial lifestyle makes them difficult to observe. As a result, little is known about their behavior, even for common species. This is especially true in the New World swifts.

The subfamily Cypseloidinae contains 12–13 species, most of which are tropical or semitropical in distribution. All are similar in body shape, and most have uniform dark plumage and facial markings, which in some are distinctive. All species in the subfamily nest in sites behind waterfalls, in caves, or deep gorges, on sea cliffs, and in sea caves. Moisture, inaccessibility

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to terrestrial predators, and darkness or at least deep shade during most of the day seem to be the rule for nest sites within the group.

The Black Swift, *Cypseloides niger*, is a widely distributed species, found locally from northwestern North America through Middle America and the West Indies (AOU 1983). Despite its wide range, most of what is known about the species is limited to information on distribution and breeding biology (Knorr 1961, Foerster and Collins 1990). In this paper aerial interactions, hostile displays, begging behavior, roosting, and possible pair bond behavior are described.

STUDY SITE AND METHODS

The biology of the Black Swift was studied in the San Jacinto Mountains in the vicinity of Idywild, Riverside Co., southern California. Most observations were conducted at a single site where an aggregation of 6–7 pairs nested every year. From 1990 to 1992, the area was visited 40 times. Visits were made at 1–15 day intervals, with observation periods ranging from 1–3 days. The area immediately surrounding the site was covered by coniferous forest. The nesting site, at 1,500 m elevation, was a cave formed by large boulders with a substantial flow of water through a side wall and several minor drips in the cave ceiling. Water flowed through the stream year-round, but substantial differences occurred among years and the flow declined from beginning to end of summer. More detailed information on the vegetation and site of the area can be found in Barbour and Major (1977) and Foerster and Collins (1990).

RESULTS AND DISCUSSION

AERIAL INTERACTIONS

For much of the breeding season (May–September) I observed the birds in several types of aerial interactions, primarily in the vicinity of the breeding site. I was able to distinguish four types of aerial interactions, not all related to courtship. The first type, which I designated as “group chase,” was a horizontal flight during which one of the birds led a high-speed chase. The leading bird (presumably a female) usually was followed by 3–6 birds; one or more of the chasing birds emitted soft high-pitched sounds. Although flight was occasionally erratic, all birds remained close together at high speeds, and the group seemed well synchronized. Group chases may involve the formation of new pairs or pair bond reinforcement. They mainly occurred early in the season.

The second kind of aerial interaction was “pair chase.” Usually, but not always, this began when a pair was moving in a continuous horizontal flight. Sometimes this type of chase split off from a group chase, with two birds separating from the group, and subsequently the birds would make a high-speed dive and follow each other closely in erratic flight maneuvers. During the dive, the birds emitted a high-pitched call that could be described as a rolling twitter. This type of chase was observed most often from the beginning to the middle of the breeding season and may function in pair bond establishment and reinforcement.

The third type of aerial interaction was “pair contact,” which also involved two birds. Usually one bird

flew horizontally, and the second bird approached from below. Next they turned over and clashed or almost touched with the feet. Sometimes one bird emitted clicking notes. After a few seconds, the higher bird changed its direction of flight, and the lower bird continued in horizontal flight. Occasionally, two birds became involved in a fourth type of aerial interaction, “touch and grasp,” in which the birds grasped each other by the feet and tumbled downward for a few meters, sometimes several meters, occasionally separating just above the vegetation. Subsequently, they rejoined the group (if any) above. Both the third and the fourth type are likely aggressive interactions.

On four dates in 1992, Black Swifts were observed in aerial interactions of the third and fourth types with Violet-green Swallows (*Tachycineta thalassina*). These aerial interactions were observed when the swifts flew over the top of the pines in a section of the canyon where a group of swallows usually foraged. When a swift approached the swallow flock, a swallow would chase the swift, and they would grasp each others' feet. Sometimes this action was just a brief dash or a short descent, with birds being grasped by the feet as in the third and fourth interaction types described above. On 8 July 1992, I photographed one of these interspecific interactions (Fig. 1). This type of interspecific aggression also occurred intraspecifically (see below).

Aerial interactions of the third and fourth types described above, in which two birds grasped each other by the feet while descending earthward, have been regarded as aerial copulations (e.g., Foerster 1987). Whether in swifts these aerial interactions are actually copulations has been controversial (Marín and Stiles 1992). In other swifts, similar interactions have been observed or photographed, but not considered copulations (Francis 1987). Copulation at the nest has been reported for many swifts in other genera, e.g., *Apus* (Moreau 1942, Lack and Lack 1952), *Chaetura* (Fischer 1958), *Collocalia* (Medway 1962), *Cypsiurus* (Fry et al. 1988), and *Streptoprocne* (Rowley and Orr 1962).

Because these aerial interactions can be interspecific, I question whether such behavior involves copulation. It is more likely that aerial interactions of types three and four are a form of aggression rather than sexual behavior. This reasoning may apply to many if not all swifts.

HOSTILE DISPLAY

The wing-raising display appears to be used to intimidate an opponent or predator. When incubating or brooding, adult Black Swifts did not leave the nest, and when I approached them closely, they reacted by raising the wings. A similar intimidation display seems to be performed by adults in many swift species, e.g., *Chaetura* spp. (Fischer 1958, Sick 1959, Snow 1962, Thompson 1977), *Cypseloides* and *Streptoprocne* spp. (Marín and Stiles 1992), and Common Swift *Apus apus* (Cramp 1985). In contrast to other swift species, in cypseloidines this display does not involve sound or vocalizations. Although the threat display is most often observed in adult swifts, this behavior can be performed by older nestlings as well. Black Swift nest-



FIGURE 1. An interspecific aerial interaction at moment of separation between Black Swift (larger bird) and Violet-green Swallow.

lings from age 18 days onward reacted to my presence by raising the wings (Fig. 2). This behavior also has been reported by Marín and Stiles (1992) for older nestlings of two *Cypseloides* species, White-chinned Swift *C. cryptus* and Spot-fronted Swift *C. cherriei*. This display apparently occurs in some nestlings of the Common Swift (*A. apus*; Lack and Lack 1952). In New World swifts, wing-raising by nestlings has been reported only in species with one-egg clutches.

In the Black Swift, only twice I observed the body-uptilting or upright threats reported for nestlings of the Spot-fronted Swift (*Cypseloides cherriei*) by Marín and Stiles (1993).

FOOD-BEGGING BEHAVIOR

Nestling Black Swifts begged silently for food when adults approached the nest; however, nestlings were aggressive towards the parents. Nestlings uplifted the outstretched wings in the same manner as the hostile display. The few observations of adult Black Swifts feeding young differ as to whether the young vocalize. Some authors do not report any nestling vocalizations, e.g., Hunter and Baldwin (1962) and Michael (1927), whereas others report some vocalizations, e.g., Smith (1928) and Murphy (1951). I did not hear nestlings vocalize, but they did raise the wings with violent moves when fed.

In altricial birds, begging is associated with arrival of parents and is usually noisy. Among New World swifts, begging is noisy and harsh in species with large clutches (e.g., *Chaetura* spp., Fischer 1958, Sick 1959,

Collins 1968, Oniki et al. 1992; White-throated Swift *Aeronautes saxatalis*, Marín unpubl. data; and Lesser Swallow-tailed Swift *Panyptila cayennensis*, Haverschmidt 1958). In the two-egg clutch species, such as *Streptoprocne* spp., begging calls are soft (Marín and Stiles 1992). In species with one-egg clutches, begging is silent (Marín and Stiles 1992; present study). These observations are consistent with Harper's (1986) prediction that begging intensity should decrease with a decrease in clutch size. However, Harper's model predicts little or no begging for broods of one chick. At least in the New World swifts, the lack of sound production is replaced by a very violent begging response. This might be explained in terms of reproductive costs and benefits. Predator attraction would be particularly costly in such species with long incubation and nestling periods, because at least in higher latitudes there would be no time to replace a grown nestling.

All adults of cypseloidines with one-egg clutches have uniformly dark plumage with distinctive facial markings. In young cypseloidines, a conspicuous bare area is present on the forehead for about 18 days after hatching. At hatching, and for the first few days of life, this area is bright pinkish in coloration. In the Black Swift, the bare spot was present until white feathers emerged on the throat and lores to cover it with white-tipped feathers. Thus, at all ages there is some light-colored or pale area around the face.

What is the significance of the bare spot and white feathering on the facial area? Once the bare spot is

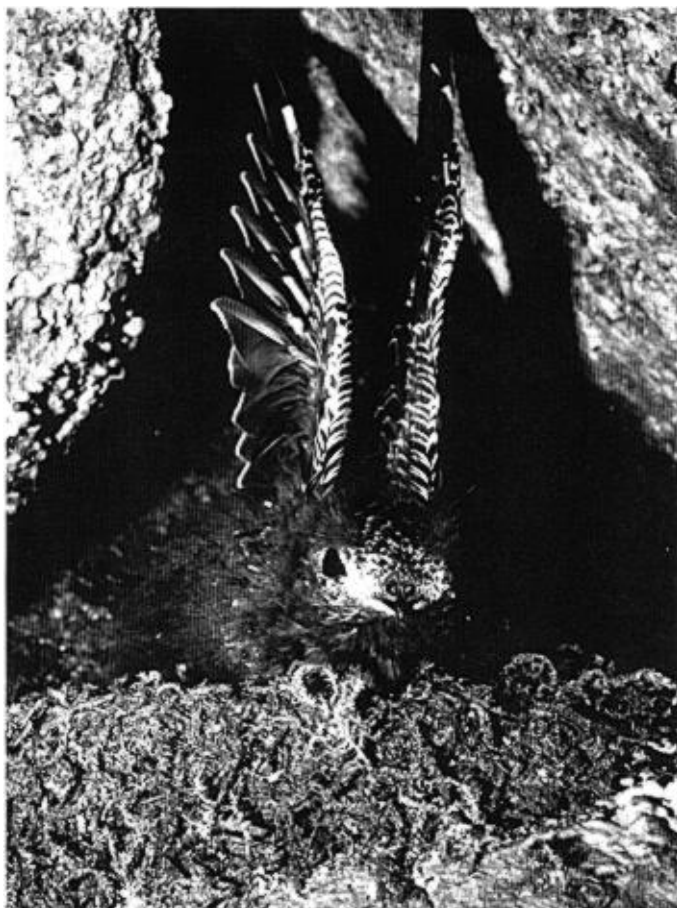


FIGURE 2. Wing-raising by young Black Swift at 27 days of age used as threat display when approached at nest. This display was given from age 18 days onward. A similar threat was used toward adults during food delivery.

covered, the white feathering that replaces it becomes conspicuous, much more so than in the adults (Fig. 3). This suggests that both the initial bare spot and the subsequent white feathering around the face may act as a signal for food transfer to the nestling, because these areas would reflect light in the dim nesting environment. The pale areas might serve two purposes: to direct the adults to the nestling's mouth and to direct the adult to the nest, especially when arriving late at night. The nestlings were very active when the parents arrived. Thus, a pale patch also may elicit a behavioral response to stimulate food transfer, which involves regurgitation of the bolus. Some supporting evidence for this hypothesis is: (1) the pale spots stand out in the dimly illuminated nesting site, (2) from about $\frac{3}{4}$ of the nestling period onward, the chicks were fed late at night, 21:00–23:00 and later, and (3) feeding was infrequent, so successful delivery of the bolus is critical (the food boluses are usually a single glue-like mass of insects).

ROOSTING

On eight occasions, I recorded the roosting habits of the Black Swift in the cave. During incubation, usually one bird roosted on the nest, and its mate sat or perched to one side with hunched body and sometimes with ruffled feathers. When young nestlings were present, both adults were observed roosting on the nest. As the nestling became older (> 20 days), only one adult roosted occasionally on the nest, and the second bird roosted on an adjacent wall (also see Murphy 1951). During the latter part of the nestling stage, both adults roosted together on the cave walls with hunched bodies and sometimes with ruffled feathers. When roosting on the walls, the birds clung to a small ledge, with their feet placed at the level of the upper breast with wings usually hanging loosely. Sometimes, the bent tail-end, but not the tips of the rachises, was used for support by spreading it like a fan. This behavior correlates with rachises that protrude less in the Black Swift than in other cypseloidine swifts. The roosting



FIGURE 3. Conspicuous white facial markings of older (> 25 days) nestlings that may aid adult to find nestling and as a target to deliver the food.

posture of *C. niger* is similar to other cypseloidine species, except the tips of the rachises are evidently used less for support (Marín and Stiles 1992).

OTHER BEHAVIORS

When a bird was incubating, it usually sat motionless when approached. Its first reaction was to droop its wing over the side of the nest, covering the egg or recently hatched chick. This reaction usually occurred before wing-raising. On many occasions during late incubation and early nestling period, the birds sat so quietly while covering the nest that when approached they did not move but instead pecked at my fingers and raised the wings. When the young were a few days old, the adults departed from the nest when I was within 1 m or so of the nest.

Several times during incubation and the early part of brooding, I observed one adult giving food to another. Only two prior accounts of food transfer between adults exist (Michael 1927, Murphy 1951). When I observed food transfer, the pair usually rotated incubation or brooding chores, and so perhaps this behavior reinforces the pair bond.

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