

SWIFT-HUNTING BEHAVIOR OF THE PEREGRINE FALCON IN ARIZONA

DAVID H. ELLIS, U. S. Geological Survey Southwest Biological Science Center, Sonoran Desert Research Station, HC 1 Box 4420, Oracle, Arizona 85623 (current address: Institute for Raptor Studies, HC 1 Box 4420, Oracle, Arizona 85623); dcellis@theriver.com

ABSTRACT: Among the solo and cooperative attacks by Peregrine Falcons (*Falco peregrinus*) on White-throated Swifts (*Aeronautes saxitalis*), the most spectacular are long series of declining stoops (sometimes involving elevational changes of up to 1 km). These repeated stoops sometimes result in falcons attempting to strike prey while climbing as well as when diving. An unspectacular technique involves swooping up, stalling, and grasping at swifts coming and going from a cleft in a cliff wall.

With all that has been published in the scientific literature about Peregrine Falcon (*Falco peregrinus*) foraging behavior (Porter et al. 1987), and all the elaborate descriptions of human-staged hunts in the falconry literature, it would seem that nothing has been left undescribed. However, the terseness required in scientific writing normally disallows the detail necessary to capture the dynamics of the falcon chase. At least two papers are exceptions to this rule in that they provide careful descriptions of entire hunting sequences. The first is Monneret's (1973) account of hunts by nesting Peregrines. The second includes accounts of using helicopters to follow hunting Peregrines and Gyrfalcons (*F. rusticolus*) (White and Nelson 1991). Dekker (1980) provided abbreviated, but compelling, descriptions of many hunts and identified at least seven methods by which Peregrines flush and/or pursue birds. Cade (1982), Bird and Aubry (1982) and various other authors (most are cited by White and Nelson [1991]) provide useful summaries of the general techniques used by Peregrines.

My focus here is to provide details of Peregrines' pursuits of White-throated Swifts (*Aeronautes saxitalis*) in Arizona. Arnold (1942) published an account of a pair of falcons capturing a White-throated Swift, but he was unsure if the predators were Peregrines or Prairie Falcons (*F. mexicanus*). It is known that other species of swifts elsewhere around the world are hunted by falcons, for example, the Hobby (*F. subbuteo*; Tinbergen 1969:199), Eleonora's Falcon (*F. eleonora*; Walter 1979), and the Bat Falcon (*F. ruficularis*; Beebe 1950). The swifts captured, however, were mostly inexperienced juveniles (Walter 1979:138–139) or weakened by prolonged storms (Tinbergen 1969). On the Colorado Plateau (Arizona, Colorado, Utah, and New Mexico) the Peregrine may eat swifts more extensively than elsewhere. In a study of Peregrine food habits on the Colorado Plateau (Ellis et al. 2004), the White-throated Swift was the species most frequently encountered among prey remains in eyries: 102 of 391 birds taken (26%) were swifts. For all of Arizona, swifts constituted 172 of 795 birds in the diet by number (22%).

Incidental to studies of Peregrine Falcon demographics (Ellis 1988) and ecology (Ellis 1982), which began in 1975, we witnessed 130 hunts (Ellis and C. T. LaRue unpubl. data), the most dramatic of which were directed

SWIFT-HUNTING BEHAVIOR OF THE PEREGRINE FALCON IN ARIZONA

at swifts. These attacks, often involving vertical distances of about 1000 m, sometimes included dozens of stoops at a single swift. Some were solo hunts; others were spectacular cooperative hunts in which the falcons often attacked the swift from both above and below.

Here I describe seven attempts by Peregrines to capture swifts and two observations of Peregrines possibly using Common Ravens (*Corvus corax*) to conceal their approach. I selected the seven attempts because each was in some way typical of a particular hunting strategy. Although these techniques are largely known from other studies, here I supply details of the attack methods.

SOLO HUNTS

Lower Reaches of the Grand Canyon of the Colorado River,
26 March 1981

Between 08:15 and 08:48, one adult male made three attempts at capture. All took place in the same general area (Figure 1) and followed the same general sequence. All were probably directed at swifts, but the distances were such that I was confident of the prey only on the first foray, described next. The Peregrine was first seen soaring up out of the abyss in front of the Supai Formation (here a wall about 120 m in height). When above the rim of the Supai (elevation ~1375 m), he crossed the canyon in a long glide (~1.3 km), then circled up to approximately the rim of the Toroweap



Figure 1. Inner gorge of the Grand Canyon of the Colorado River and site where a male Peregrine Falcon pursued a White-throated Swift for a vertical kilometer on 26 March 1981.

SWIFT-HUNTING BEHAVIOR OF THE PEREGRINE FALCON IN ARIZONA

Formation (elevation 1750 m). After soaring another ~1.5 km south, he swept his wings back and dropped into a dive at ~30° below horizontal. After stooping ~0.4 km to mid canyon, he suddenly turned sharply downward and plunged vertically ~300 m until flashing past the swift. The falcon then pulled sharply out of the stoop and, with wings pumping, shot up ~100 m. As soon as he started to slow because of gravity, he began deep, rapid flaps and passed inverted across the zenith of his ascent. By crossing the apex upside down, he was able to put the full force of his wings into fighting centrifugal force, decreasing the radius of his overhead arch, and maintaining speed for the next plunge. His second stoop took him down the face of the Redwall Limestone and out of sight into the canyon. The outcome of the attack was not seen, but within 5 minutes he was again soaring up the Supai Formation without prey. The vertical distance between the onset of the first stoop and the nadir of the second was ~1000 m (910 m in one estimate based on visual approximations using 185 m as the height of the Redwall Limestone and 1070 m in a second estimate based on elevations on USGS topographic sheets).

Salt Eyrie, Central Arizona, 18 July 1978

Some solo hunts are almost as spectacular as the most dramatic cooperative attempts. At the opposite extreme, however, was a series of solo attempts by an adult female to catch swifts entering and leaving a long vertical crack in the quartzite cliff only ~60 m below her eyrie. I watched the site from 07:00 to ~19:50. During that time, two adults and one well-fledged juvenile were around the eyrie. From 19:20 to 19:25, the adult female swooped up to the crack, stalled, fell away without prey, swooped out from the cliff wall to gain speed, then turned and, flapping, rose up again to the crack, this time grasping prey which she delivered to the screaming juvenile on a pinnacle ~200 m away.

Between 19:25 and 19:32, the female visited three perches and passed back and forth along the rim of the eyrie cliff. At 19:32, she returned to the crack and made four more pendulum-like sorties against the wall, all in apparent efforts to snatch swifts. In each of these attempts, she swooped up to the crack, stalled, and, with a few fluttering wing strokes, grabbed at passing swifts. Then she turned, fell away from the cliff, and swooped downward and out ~30 m while flapping and gathering speed. Then, rising up, she used her momentum to turn back up toward the cliff and, while flapping, rose up again to the crack, stalled, and again tried to grasp a swift. After the fourth attempt, she flew to a boulder on the steep hillside and, apparently without prey, perched until it was too dark for me to see her departure.

POSSIBLE USE OF A RAVEN AS A BEATER

Glen Canyon of the Colorado River, Northern Arizona, 25 March 1982

Peregrine Falcons have long been known to use other birds or even machines (Bishop and Bishop 1972, Ellis et al. 1993) to flush prey or to conceal the falcon's approach to prey. In the canyon country of northern Arizona, it is normal to see two Common Ravens passing in tandem along the cliff

SWIFT-HUNTING BEHAVIOR OF THE PEREGRINE FALCON IN ARIZONA

walls. The second raven very often trails the first by roughly 20–100 m. Twice on 25 March 1982 I saw an adult female Peregrine Falcon patrolling the canyon rim, trailing about 100 m behind a raven. So routine is it to see two ravens in tandem that, after noting that the first bird was a raven, I gave the second bird hardly a glance (expecting it to also be a raven), but in that brief glance, saw the falcon. Although I did not see her dive on prey from this position, I suspected that following the raven was a hunting tactic. The raven showed no alarm or avoidance at having the falcon in tow.

COOPERATIVE ATTEMPTS AT SWIFTS

Great Wall Eyrie, Southeastern Arizona, 4 March 1980, 16:54

Both adults dived off the cliff (175 m tall) where they nested (Figure 2) and, with a few rapid wing beats, plunged diagonally downward at a swift then flying horizontally at only ~15 m above the canopy of oaks at the base of the cliff. After the first attempt, the adults timed their attacks so that they crossed the trajectory of the swift almost simultaneously: one falcon shooting up vertically at the swift while the second falcon plunged vertically from above. Again and again the pair passed through the swift's path until, after six such attempts, the swift disappeared among the oaks. During these attacks, the top-to-bottom diameter of each loop described by the falcons was ~100–150 m. The female righted herself at the top of each loop, but



Figure 2. Adult Peregrine Falcon at an eyrie in southeastern Arizona where swifts are commonly taken as prey.

SWIFT-HUNTING BEHAVIOR OF THE PEREGRINE FALCON IN ARIZONA

the male, rather than disrupt the flow of his motion, crossed the top of each loop with his underparts skyward, then plunged downward again for another attempt at the swift. The falcons flapped mostly just after the top of each loop as they gained speed for the next plunge.

Grand Canyon of the Colorado River, Hance Rapids, 19 March 1977

At about 10:00, two adult Peregrine Falcons swept down from a side canyon, north toward the river, and entered the inner gorge in relentless flapping pursuit of a swift. The swift was fluttering along erratically only ~10–15 m above the dunes and rock piles. After each adult stooped ~12 times, the swift crashed into the boulders on the north side of the river. The Peregrines showed no interest in pursuing the fallen swift but flew to separate perches near the rim of the Hakatai Formation.

After nearly a half hour without activity, both adults, with rapid wing beats, leaped off the cliffs and intercepted another swift low over the dunes. Each bird, in roller-coaster dives (each loop ~70–100 m in diameter), stooped at the swift ~15 times. The swift, although flapping furiously, made only slow forward progress during the attack, perhaps only 50 m forward for each stoop of a falcon. Occasionally one falcon continued across the apex of its stoop with its body inverted (belly to the sun). Finally, the harried prey plunged into the Colorado River near mid-stream. Each adult falcon then, in slow flapping flight, passed over the downed bird about five times before the female grabbed the prey and flew down river out of sight.

Glen Canyon, North-Central Arizona, 25 March 1982

Surely this was the most persistent attack I ever witnessed. While hiking along the rim of the canyon, I first noted the adult female Peregrine arrive. She came in from the north and circled up high over the rim. Within 1 minute, I saw the male also circling overhead but much higher than the female. At 12:42, the male began a long, shallow, flapping stoop to the north. The female followed. Between 12:42 and 12:48, both birds stooped again and again at a swift about 15 m below the canyon rim. Time after time, the male plunged down toward the swift, then, having missed, shot upward trying to make contact while on the rise. Each cycle occupied ~100 m from crest to trough. The female also stooped again and again, but her circles were only about 25 m in diameter, so she actually made approximately 2.5 cycles to one by the male. After about 20 cycles by the male and about 40–50 by the female, the swift disappeared; both birds broke off the chase and began soaring up over the canyon. By 12:50, the male and female were seen south of the canyon pursuing another swift. After only a few stoops, the birds dropped out of sight behind an intervening hill but soon reappeared, this time with the female clutching a swift. While on the wing soaring above the canyon, she plucked and consumed the swift (until 13:05). During her meal, she was pursued by two ravens in a shallow stoop extending nearly 1 km. The nearest raven briefly drew within 20 m of the female. Her facility in evading the ravens was attested by her continuing to pluck and feed even while one raven was still in pursuit.

SWIFT-HUNTING BEHAVIOR OF THE PEREGRINE FALCON IN ARIZONA

BEHAVIOR OF SWIFTS

When using high-amplitude stoops, either while hunting solo or in tandem, the falcons' first attacks normally occurred with the swift well exposed, far from cover. Thereafter, the swifts typically seemed vulnerable, but they may have been difficult to capture as they paddled erratically about with rapid wing beats, body teetering from side to side, at what appeared to be rather slow forward speed. The secondary strategy in many attacks was to approach the ground or a cliff face closely, in an apparent effort to thwart the attack by increasing the risk to the falcon of colliding with the terrain. The ultimate result of this tactic was seen in the Hance Rapids observations of 1977 when one swift plunged into the boulders and another into the water.

DISCUSSION

In Arizona, Peregrine Falcons use a variety of tactics to hunt swifts, the most common being long high-speed stoops from high above. I never saw the kind of "tail chase" pursuit observed by Arnold (1942). This suggests to me that the raptors he observed were Prairie Falcons, not Peregrines, a more likely choice given the location (a hot, dry, desert environment far from permanent water).

The male Peregrines seemed much more agile than the larger females, as attested by their often maintaining speed in each stoop-climb cycle by crossing the zenith of some loops inverted and flapping furiously to maintain speed. I would have expected the larger females to describe loops of larger diameter than did the males, but not so; the females sometimes flew traveling loops ~25 m in diameter (from zenith to nadir) with the strike at the swift occurring only at the bottom. The males, by contrast, normally flew loops up to 100 m in diameter and more frequently struck twice in each loop, once in crossing the swift's trajectory while plunging vertically downward and again while shooting vertically upward.

The sounds accompanying these attacks add much to the spectacle. The whistling roar of the falcon begins as it reaches maximum velocity plunging downward, but the roar is loudest and changes to a sound like the ripping of a great canvas sail when, for a few seconds, the falcon arches, countering the downward momentum of its dive, and, forcing its wings against the centrifugal force of the arc, curves skyward.

ACKNOWLEDGMENTS

Many of my swift-hunting observations were made while I was employed by the Patuxent Wildlife Research Center. The Southwest Biological Science Center financed the write-up, and the National Aeronautics and Space Administration financed publication. The interpretation of my observations profited from discussions (some in the field) with James K. Fackler and Charles T. LaRue. R. Wayne Nelson helped greatly with the literature and in restructuring my descriptions of the attacks. Charles Collins, Tim Manolis, and Clayton White improved the text.

SWIFT-HUNTING BEHAVIOR OF THE PEREGRINE FALCON IN ARIZONA

LITERATURE CITED

- Arnold, L. W. 1942. The aerial capture of a White-throated Swift by a pair of falcons. *Condor* 44:280.
- Beebe, W. 1950. Home life of the Bat Falcon *Falco albicularis albicularis* Daudin. *Zoologica* 35(4):69–86.
- Bird, D. M., and Aubry, Y. 1982. Reproductive and hunting behavior in Peregrine Falcons, *Falco peregrinus*, in southern Quebec. *Can. Field-Nat.* 96:167–171.
- Bishop, Y., and Bishop, R. 1972. Predation of birds along railway lines. *Australian Bird Watcher* 4:223–224.
- Cade, T. J. 1982. *The Falcons of the World*. Comstock/Cornell Univ. Press, New York.
- Dekker, D. 1980. Hunting success rates, foraging habits, and prey selection of Peregrine Falcons migrating through central Alberta. *Can. Field-Nat.* 94:371–382.
- Ellis, D. H. 1982. The Peregrine Falcon in Arizona: Habitat utilization and management recommendations. *Inst. for Raptor Studies Res. Rep.* 1.
- Ellis, D. H. 1988. Distribution, productivity, and status of the Peregrine Falcon in Arizona, in *Peregrine Falcon Populations: Their Management and Recovery* (T. J. Cade, J. H. Enderson, C. G. Thelander, and C. M. White, eds.), pp. 87–94. *The Peregrine Fund*, Boise, ID.
- Ellis, D. H., Bednarz, J. C., Smith, D. G., and Flemming, S. P. 1993. Social foraging classes in raptorial birds. *BioScience* 43:14–20.
- Ellis, D. H., Ellis, C. H., Sabo, B. A., Rea, A. M., Dawson, J., Fackler, J. K., LaRue, C. T., Grubb, T. G., Schmitt, J., Smith, D. G., and Kéry, M. 2004. Summer diet of the Peregrine Falcon in faunistically rich and poor zones of Arizona analyzed with capture–recapture modeling. *Condor* 106:873–886.
- Monneret, R.-J. 1973. Techniques de chasse du faucon pèlerin *Falco peregrinus* dans une région de Moyenne Montagne. *Alauda* 41:403–412.
- Porter, R. D., Jenkins, M. A., and Gaski, A. L. 1987. Working bibliography of the Peregrine Falcon. *Natl. Wildlife Fed. Sci. Tech. Ser.* 9.
- Tinbergen, N. 1969. *Curious Naturalist*. Anchor Books/Doubleday, Garden City, NY.
- Walter, H. 1979. *Eleonora's Falcon: Adaptation to Prey and Habitat in a Social Raptor*. Univ. Chicago Press, Chicago.
- White, C. M., and Nelson, R. W. 1991. Hunting range and strategies in a tundra-breeding Peregrine and Gyrfalcon observed from a helicopter. *J. Raptor Res.* 25:49–62.

Accepted 25 April 2006