THE ATTACK AND STRIKE OF SOME NORTH AMERICAN RAPTORS

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Qualitative observations of the attack and strike of raptorial birds are numerous, but few quantitative measurements are available of the velocity, descent, acceleration, and deceleration of the pelvis, legs, and feet. My anatomical studies of the adaptations of the pelvic limb of selected species of North American birds of prey (MS) led to the present study because an understanding of how raptors use their feet and legs during the attack and strike facilitates the interpretation of anatomical differences. I used cinematography as a means of recording these data accurately (Hildebrand, 1963, 1964).

The data presented here are somewhat limited. As the prey species were loosely tethered to the ground or a piece of canvas some distance from the raptor, the prey situations presented to the predator were not so varied nor were the prey so active as those normally encountered. Secondly although some variety of prey species was used, it was not possible to present each hawk or falcon with many different kinds. A given species of raptor captures a diversity of prey: Beebe (1960) and Storer (1966) indicate that the accipters and falcons are opportunists, preying upon those animals available and most easily secured. Possibly hawks and falcons attack and strike larger prey in a different manner than they do smaller ones. Lastly, an individual bird may employ a variety of hunting, attacking, and striking attitudes not characteristic for its particular species (Cade, 1960; White, 1962; Mead, 1963).

Materials and Methods

I photographed the attack and strike of six species of raptors. The falcons and hawks studied had been trained for falconry. I used a Traid Photo-Sonics 16-1B electric camera at film speeds from 800 to 1000 fps and exposures from 1/3000th to 1/5000th of a second. Precise determinations of film speed were made possible by a timing light that marked the margin of the film at intervals of one millisecond. The hawks and large falcons were filmed at a distance of 30 feet using a Navitar 90 mm f/1.9 lens. Sparrow Hawks (*Falco sparverius*) were filmed with a 15 mm f/2.3 lens at a distance of 42 inches.

With the exception of Prairie Falcons (*F. mexicanus*) and Peregrine Falcons (*F. peregrinus*), the birds were filmed against a background 6 feet high and 13 feet long on which was ruled a grid of 10-cm squares. To facilitate measurements for the smaller species (*F. sparverius*), the grid was altered to 5 cm wide by 10 cm high.

The circumstances at the time of the recorded strike were similar for the accipiters and Red-tailed Hawks (*Buteo jamaicensis*). The prey was tethered loosely 3 feet in front of the grid. The camera was mounted at right angles to the grid and the hawk was released from a point parallel to the grid and at least 40 feet from the prey. *F. sparverius* was filmed under slightly different conditions: the prey was tethered 16 inches from the grid and 13–15 feet from the hawk. The hawk flew parallel to the grid from a perch 5 feet high.

The attack behavior of *F. mexicanus* and *F. peregrinus* prevented the use of a grid. The falcon was released before the prey was shown, and characteristically the bird flew to a height usually greater than 50 feet and began circling. Upon signal the prey (a blindfolded pigeon) was released and usually flew upward. The falcon struck the prey at variable distances from the ground and camera.

I determined by manipulation the functional pivot points of the hip (iliofemoral) joint, knee (femorotibial) joint, and heel (intertarsal) joint of each living raptor filmed, and measured the distances between these points to the nearest millimeter. The acetabulum was measured from the posterior margin of the tail feathers. The position of the scapulohumeral (shoulder) joint was estimated on the photographs by eye. These measurements enabled me to estimate the instantaneous position of the leg bones during a frame by frame analysis. Tracing the displacement of these bones and the changes of the angles of the joints was the basis for an analysis of changes in velocity, acceleration, and deceleration. The raptor's position relative to the grid and camera lens causes a parallax, or difference between the apparent and actual distance the bird moves. This error was corrected by the use of similar triangles. Joint angles for strikes not parallel to the camera lens were not measured.

RESULTS

Table 1 lists several of the variables that occur at the time of the strike. The heel joint, knee joint, body axis to femur (hip) and body axis to horizontal angles were measured at the time of impact with the prey. These angles varied substantially within individuals and species depending on the raptor's position and awareness at the time the prey was introduced. Nevertheless the ranges of the angles measured show several distinct patterns. The body axis of the bird passes through both the scapulohumeral joint and the acetabulum.

Accipiter cooperii.—I analyzed four strikes (110 feet of film) of one adult female Cooper's Hawk. The prey used were Starlings (*Sturnus vulgaris*) and Rock Doves (*Columba livia*). Table 1 gives average measurements of two strikes at Starlings. In two typical sequences, the hawk ceased its flapping flight 12 to 15 feet from the prey, and 5 feet from contact began swinging the legs forward accompanied by a moderate amount of extension. Thus the feet attained velocities of 1140 cm/sec (25 mph), 15 per cent greater than that of the pelvis. Component velocities show that almost 100 per cent of the velocity of the feet was in the horizontal plane at the time of impact. At the moment of contact the hawk set its wings in a braking position, held the toes in an extended position, and maintained a body axis to horizontal angle approaching 80°. One strike was made with the right foot only.

Variations of this strike posture were seen in two sequences in which

TABLE 1

VELOCITIES AND ANGLES OF THE PELVIC LIMB JOINTS OF RAPTORS AT THE TIME OF STRIKE

Species	Heel	Knee	Body axis-femur	Body axis-horizontal	Mean strike velocity (cm/sec)		Component velocity (cm/sec)		PV/FV[1]
					Head	Feet	Horizontal	Vertical	
A. cooperii (2)	146–150°	119–123°	70–80°	77–82°	480	1,140	1,130	10	85%
A. gentilis (3)	150–156	140–146	80–90	87–95	1,400	2,250	2,100	150	85
B. jamaicensis (5)	130–142	117–141	55–81	76–87	425	650	650	0	85
F. mexicanus (3)	60–130	120–150	70–90	50–90	1,460	–	–	–	–
F. peregrinus (2)	60–80	120–140	50–60	70–90	–	–	–	–	–
F. sparverius (2)	150–165	145–153	109–113	82–85	275	585	290	295	80

[1] PV, velocity of the pelvis; FV, velocity of the feet.

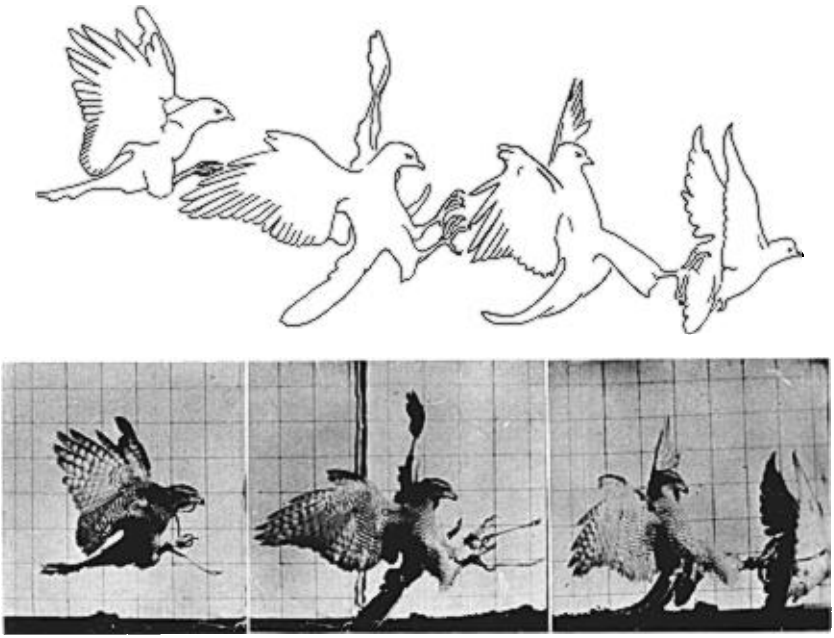

Figure 1. Typical striking posture of *A. gentilis*. Tracings (above) were made for analysis from 16-mm film or prints (below). Images are spaced at 30-msec intervals. See text for complete description of strike.

the Cooper's Hawk attacked a pigeon from behind and below. The angle of ascent of the raptor from the horizontal was 70°. Just prior to contact the hawk set its wings and swung its pelvis through an arc that produced a body axis to horizontal angle of 180°. It extended its legs in a characteristic manner at impact, but appeared to be lying on its back in the air. A similar strike posture is described by Bent (1937: 119), but it is not clear whether the hawk "rolled over" on its back, thus keeping its head farthest anterior at all times, or whether the pelvis was swung forward as above. Flapping enabled the hawk recorded on film to right itself, bank, and descend while holding firmly to the pigeon.

Accipiter gentilis.—I analyzed seven strikes at pigeons (270 feet of film) by two adult female Goshawks. Table 1 gives average measurements of three strikes. In the approach flight the Goshawks moved their wings through complete flapping cycles of marked amplitude. They ceased flapping 25–30 feet from the prey and set their wings into a gliding position; 5–8 feet from the target they began to lower their feet, with the toes still partially flexed. At impact the legs were substantially extended and the feet well out in front of the attacking bird (Figure 1).

The toes were fully extended 30–35 inches from the prey. At the instant of impact, feet velocities of 2250 cm/sec (50 mph) were recorded, which was 15 per cent greater than that of the pelvis. Most of the total velocity of the feet was in the horizontal plane. At impact the pelvis averaged a velocity 30 per cent greater than that of the head.

Just before contact these raptors placed the wings and tail into a maximal braking position. Initial contact was made with one foot in four of the seven strikes recorded. In those instances toes of the free foot were closed tightly from 20–25 msec following impact.

The Goshawks moved the pelvis laterally relative to the apparent trajectory in four of the recorded attacks. In such instances the acute angle formed by the vertebral column and the ground approached 60° at the moment of contact with the prey. Following impact the raptors thrust their wings up and forward as their momentum carried them and the prey for some distance horizontally. Postimpact rotation about the axis of the spine was often marked during this period and was accentuated when contact with the prey was made with one foot. In the attack shown (Figure 1) the bird rotated its body around the vertically oriented vertebral column through 270° following the strike.

Accipiters characteristically use a kneading action with the talons to kill their prey. Analyses of the events following the strike reveal the rapid initiation of this behavior; the Goshawk shown began kneading 0.75 seconds after impact.

Buteo jamaicensis.—I collected data from eight recorded attacks and strikes (135 feet of film) of two immature and one adult Red-tailed Hawks. Prey included ground squirrels (*Spermophilis beechyei*), pigeons, and a lure. A lure is an object on the end of a long cord used in falconry to recall the hawk. It is often baited with food. *B. jamaicensis* seems to strike the lure and living prey similarly.

The data recorded in Table 1 are based on five strikes. *B. jamaicensis* often resembled the accipiters in its attack flight except for the Red-tail's slower speed. The hawks set their wings in a gliding position 10–15 feet from the prey and began lowering their legs approximately 10 feet before contact. The degree of leg extension at impact varied substantially among the three individuals studied, but the body axis to horizontal angle remained less than 90° in all cases. These raptors extended their toes relatively late, averaging 12 msec before contact. The feet velocity of 650 cm/sec (12 mph) recorded at impact was 15 per cent greater than the velocity of the pelvis. A small vertical component is indicated in relation to the horizontal component.

The hawks kept their eyes fixed on the intended prey during the attack,

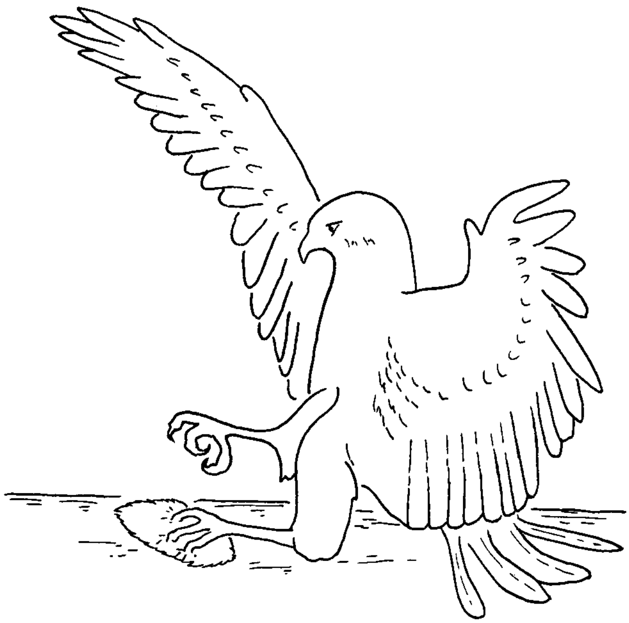

Figure 2. Postimpact posture of *B. jamaicensis*. Note the tarsometatarsus on the horizontal and the forward thrust of the wings. Possibly this behavior minimizes the raptors forward movement following a strike. See text for a more complete description.

an attitude characteristic for all the diurnal raptors studied. The trajectory of the head remained relatively straight as the pelvis was brought forward, the axis for the change in pitch passing through the shoulders. These birds displaced the pelvis laterally during its forward swing in some instances and grasped with one foot in two of the eight strikes. The toes of the free foot were closed tightly 22 and 32 msec following contact. Postimpact rotation about the vertically oriented vertebral column was seen in three strikes.

The hawk dropped to its heel after securing the prey in three instances, which placed the tarsometatarsus on the horizontal. The hawk's momentum tended to carry it forward after impact, but it minimized this movement by thrusting its wings forward and using the tarsometatarsus as a lever to push against (Figure 2).

The prey's posture and orientation just prior to the strike had an effect on the placement of the feet of the attacking raptors. If the prey was oriented across or perpendicular to the line of attack, the hawk struck

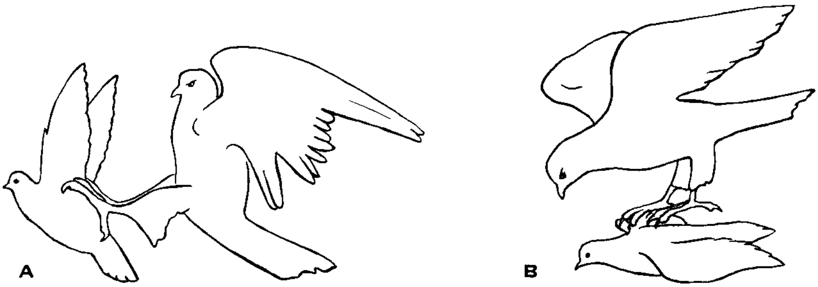

Figure 3. The two typical strike postures of *F. mexicanus* and *F. peregrinus*. Left: position of the body of the falcon relative to its legs when the falcon maintains a grip on the prey following contact. Right: position of the body of the falcon relative to its legs at the moment it delivers a glancing strike in a stoop.

simultaneously with both feet. If the prey was oriented parallel to the line of attack, the hawk placed a lead foot on or just behind the prey's head 15, 20, and 25 msec before it placed its second foot farther back. The raptors maintained balance during this differential placement of the feet by appropriate wing compensations; in those instances where the right foot was the lead foot, the hawks sharply flexed the right wing and fully extended the left. These raptors made successful compensations in the last second of flight according to the prey's behavior.

Falco mexicanus.—I recorded seven strikes (170 feet of film) of two immature female and one immature male Prairie Falcons. Five strikes were made at pigeons and two at a swinging lure. The data presented in Table 1 are based on the analysis of three strikes of the two females. *F. mexicanus* and *F. peregrinus* often "stoop" or descend on the prey from a high vantage point. The blow delivered is of short duration, as the raptor does not retain a grip on the prey. The postimpact flight of the falcon is usually in a short semicircle back to the prey, presumably in preparation for a second strike if necessary. Unfortunately I was unable to record this behavioral pattern on film for *F. mexicanus*. Thus the strikes filmed represent a diffent strike pattern in which the falcon approached relatively level with the prey and apparently attempted to cling to it after contact. When successful the falcon carried the prey to the ground.

These falcons continued to beat their wings in a steady but shallow stroke until they were within a few feet of the prey. In one instance the bird set its wings as late as 80 msec before contact. Forward movement of the feet and pelvis began from 80 to 140 msec before impact. The toes were fully extended during this time, and the wings were sharply flexed and positioned above the head (Figure 3A). The body axis to horizontal angle approached 90°, which placed most of the raptor's weight behind its feet.

These falcons rotated the pelvis forward very rapidly during this strike pattern, though accurate velocity measurements could not be made (see Methods). A strike was made with one foot in one instance, and the toes of the free foot were completely closed 10 msec after contact.

Falco peregrinus.—I studied eight strikes (170 feet of film) of three immature female Peregrine Falcons at pigeons (two *F. p. anatum* and one *F. p. pealei*). Both the stoop and level pursuit were recorded. In those instances where *F. peregrinus* held onto the prey after impact, its approach and strike pattern closely resembled that described above for *F. mexicanus*. The falcons pumped their wings in a shallow beat until they began to lower their legs and pelvis. Times recorded in four instances for descent of the pelvis were 60, 60, 85, and 100 msec before contact. These falcons placed their wings in a partial brake position as the pelvic region moved forward. The preimpact brake pattern recorded for *F. mexicanus* and *F. peregrinus* was ordinarily much less marked than those of the accipiters and *B. jamaicensis*.

When stooping, the Peregrines did not seem to try to hold onto their prey, but only to strike it. They approached the prey from above with their legs relatively more flexed at contact (Figure 3B), and maintained a body axis to horizontal angle of much less than 90°. This posture permitted a glancing strike at the prey, and the birds did not place their full body weight behind their feet. In two instances they began lowering their feet and extending their toes 84–100 msec before impact. These raptors struck with all four toes completely extended in all recorded contacts. At impact the toes were immediately closed, but the speed at which the falcons were flying made contact time with the prey very brief. The times noted for completely closed toes of the first foot coming off the prey were 20 and 30 msec following impact. Contact times for the above two strikes were 100 and 30 msec respectively. In both instances the prey was knocked to the ground. Body velocities of Peregrine Falcons at the time of strike were calculated (not precisely; see Methods) to be slightly above 40 mph.

Falco sparverius.—My extensive field observations of this species show its attack and strike to be rather varied. The data in Table 1 are very limited as they are based upon only two strikes (45 feet of film) of one female Sparrow Hawk at a deer mouse (*Peromyscus maniculatus*). The bird's angle of descent at the prey was characteristically steep. Often during the attack the wings were partially flexed and the hawk seemed to be free falling. Just before impact the bird spread its wings in the typical *Accipiter-Buteo* brake position. As it brought its pelvis forward it moved its partially extended legs to a position beneath the beak. At this time the toes were only partly extended, and the falcon did not extend them fully until it accelerated its legs forward and downward toward the prey. In one instance full extension did not occur until 25 msec before contact. Feet velocities were 20 per cent greater than those of the pelvis, indicating a marked downward thrust of the feet at the time of contact. The falcon dropped to its heel following impact, but immediately bounced back to a standing position in the two recorded instances. The wings were thrown high and forward after contact.

Discussion

In addition to possible limitations previously mentioned, it is important to point out that 1) the raptors filmed were trained and maintained for falconry and characteristically did not exercise as frequently as wild birds and 2) they were allowed to fly only when very hungry. Hence the birds photographed may not have been as physically fit as the norm of their species, but they may have been more highly motivated by more intense physiological drives. I do not know what influence these factors had on my results.

The accipiters capture a large number of birds for food, depending somewhat on the prey species available (Meng, 1959; Storer, 1966). The ability of a flying hawk to capture small and large birds in flight presupposes the raptor to be either very fast, deftly maneuverable, or both. Ornithologists have long been aware that the accipters' broad wings and long tail give them maneuverability. Peczely (1964) found anatomical support for this upon examination of the thoracic vertebrae of select species of accipiters. The heavy elastic ligaments and wide articular capsules (relative to other raptors studied) were noted as adaptations for supple flight. An attack of a Goshawk I recorded on film as the bird flew toward the camera is particularly revealing of this species' agility. Flying rather slowly in pursuit of a loosely tethered pigeon missed during an initial attack, the Goshawk suddenly had to change its body orientation about the longitudinal axis (roll). It elevated both wings together, and during the downstroke it depressed the right wing faster and deeper than the left, so that its body rolled through 110° in 35 msec.

The Cooper's Hawk and Goshawk show marked forward thrust of the pelvis and rapid extension of the legs just before impact. This technique uses body speed to increase shocking power. The shock delivered must be substantial, as the vertebral column is almost vertically oriented, the feet are held chest-high, and much of the hawk's weight is directly behind the extended toes. This basic posture and their substantial agility in flight add to the accipiters' efficiency as predators.

The accipiters and *B. jamaicensis* have similar striking postures, though velocities of the trunk, pelvis, and feet differ markedly in the two genera. Predator and prey studies of the Red-tailed Hawk (Fitch et al., 1946) support the generally held belief that this species is not adept at capturing healthy flying birds. There are exceptions, but the general pattern is evident. The data presented here show that the approach flight, pelvis swing, and leg extensions are slower for the Red-tailed Hawk than for the accipiters. Thus the relative shock delivered to the prey at impact is not so great as that delivered by the Cooper's Hawk or the Goshawk. This may explain, in part at least, why the Red-tailed Hawk, even though averaging by weight 10 per cent larger in males and 17 per cent larger in females than *A. gentilis,* often preys upon smaller species (Fitch et al., 1946; Craighead and Craighead, 1956; Meng, 1959; Storer, 1966).

Both the accipiters and *B. jamaicensis* demonstrated marked compensatory movements of their feet and wings just before impact. These adjustments, made in milliseconds, are dependent on the movements of the prey during the attack. A predator's ability to react to last instant evasion tacks and sudden defense postures by its prey has distinct selective advantages.

It has been noted that *B. jamaicensis* often stops its horizontal movement just after impact with the prey by dropping down upon its tarsometatarsus and leaning forward. The resulting leverage undoubtedly helps the braking wings bring predator and prey to a sudden stop. A prolonged postimpact horizontal movement in foliage could be hazardous to the raptor. I have film showing this behavior consistently following the strike of the Barn Owl (*Tyto alba*), and to a lesser extent of the Screech Owl (*Otus asio*) and Burrowing Owl (*Speotyto alba*).

The two species of large falcons exhibited two distinct striking postures. The first, in which the falcon presumably attempted to cling to its prey, was similar to that of the accipiters and the Red-tail. This posture might be used with prey small enough to be grasped and carried to the ground, and also when the falcon's approach flight relative to the prey's position and direction of movement is such that injury to the raptor upon impact is unlikely.

The second striking posture is the common and classic "stoop" of *F. peregrinus* that delivers a glancing blow of short duration. This posture differs markedly from the one described previously in that the pelvis is not swung through so far, and thus the weight of the falcon is not placed directly behind the striking feet. Though the toes are closed immediately on impact, the brief contact period limits the degree of piercing and tearing possible with the foretalons, yet the speed and direction of movement appear optimum for effectiveness of the hind talon (hallux). Bond (1936) notes that both falcons employ this method when attacking mammals too large to seize safely and reports that they strike at the animal's head and neck in a series of stoops until the prey can be handled. An important aspect of the short-duration strike is the optimal positioning of the hallux. Several authors attest to the severity of wounds inflicted after only one such contact (Bond, 1936; Bent, 1938). The coordination necessary for these falcons to adjust angles and make compensations, to stoop effectively upon a moving prey is remarkable in itself, to say nothing of the timing required to inflict a telling wound so quickly. In two instances *F. peregrinus* almost incapacitated pigeons in contacts lasting only 30 and 100 msec.

My data for striking postures of falcons do not agree with those of Peczely (1964). How he arrived at the posture figured (p. 112) is not clear, but at the moment of contact with the prey for *Falco* sp. he shows the femorotibial (knee) and intertarsal (heel) joints extended beyond their anatomical limits.

F. sparverius is an active species often seen on an open perch from which it makes short, rapid sallies at its prey. The attack and strike of *F. sparverius* differ from those of the two larger falcons. Vertical displacement of the body and feet is evident during the attack. Heintzelman (1964) found the diet of this species to consist of a high percentage of insects and small mammals, prey species that are generally found in and under vegetative cover, and for hunting which a vertical vantage point and steep angle of attack are highly advantageous.

The wings and tail are placed into a high drag position just before impact in all the species studied. The significance of such behavior may be several fold. Placing the wings into the braking position makes the body move around an axis that passes through the shoulder joints. The resulting positive pitch movements facilitate the forward thrust of the pelvis and legs just before contact. The average velocities of the pelvis relative to the head were 50 per cent faster for *A. cooperii*, 30 per cent faster for *A. gentilis*, 25 per cent faster for *B. jamaicensis*, and 40 per cent faster for *F. sparverius*. Feet velocities 15 per cent higher than the pelvis velocity for these species were normal. Also the fully extended wings and tail serve to decelerate the head and may help the predator make compensatory movement successfully just before the strike.

Strikes with one foot were recorded for *B. jamaicensis*, *A. cooperii*, *A. gentilis*, and *F. mexicanus*. The significance of this is not clear. Fisher

(1957), in his study of footedness in pigeons, found that individual birds often favored one foot as a lead when landing. Whether raptors favor one foot for striking to the same extent is not known. In some cases where contact was made with one foot (*A. cooperii, A. gentilis, B. jamaicensis*), the bird used the free foot on the ground to help maintain postimpact balance.

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SUMMARY

Two basic patterns of attack are noted. The Cooper's Hawk, Goshawk, and Red-tailed Hawk demonstrate the first wherein the greatest displacement during the attack is along the horizontal. The Peregrine and Prairie Falcons use this pattern also, but their attack varies according to the falcon's position relative to the prey when the attack starts. A distinctive variation for these large falcons is the classic "stoop," which results in an impact of very short duration with all four toes fully extended at contact. In all these birds the major component of velocity of the feet is in a horizontal direction at the time of impact. In the second pattern, shown by the Sparrow Hawk, the vertical displacement of the body and feet is evident during the attack, and there is very little movement forward.

Four of the species studied made one or more strikes with one foot. The legs of the raptor tend to extend markedly just before contact with the prey. In most instances this extension is at a velocity 15 per cent greater than that of the pelvis. The toes of most species are fully extended just a few feet and a few milliseconds before impact.

Raptors demonstrate a high degree of coordination. Adjustments of the pelvic limbs and associated structures in the attack and strike are often only milliseconds in duration. The selective advantage of such rapid movements and compensatory patterns are great.

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