A DIFFERENCE IN PREY SELECTION BY ADULT AND IMMATURE PEREGRINE FALCONS DURING AUTUMN MIGRATION

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ABSTRACT

Avian prey captured by immature Peregrine Falcons during autumn migration at Assateague Island, MD/VA, consisted mostly of solitary migrant birds (94.2%), especially Common (Yellow-shafted) Flickers (37.2%). Adult Peregrines, however, took about equal numbers of flocking shorebird and other bird species. Probable reasons for the disparity were differences in daily hunting activity (immatures catch prey early in the day); aerodynamic differences between the age classes (adults have heavier wing-loading); experience in catching prey (a flock of shorebirds confuses an immature falcon); and development of specific search images for shorebirds by adult Peregrines.

INTRODUCTION

Difference in the types of prey captured by immatures and adults of the same species are well documented for many taxa, especially fish, amphibians and reptiles. Usually, fish fry and frog tadpoles do not compete with adults for food resources. Clark & Gibbons (1969) reported a shift from a carnivorous to a mostly herbivorous diet from youth to maturity in Yellow-bellied Turtles (*Pseudemys scripta*). Young versus old Yarrow's Spiny Lizards (*Sceloporus jarrovi*) differ in activity periods, and in selection of perches and prey items (Simon 1976). Such resource partitioning or niche segregation has been interpreted as an adaptation to reduce competiton (intraspecific or interspecific), thus allowing a greater number of individuals to coexist within a habitat.

Most examples of intraspecific resource partitioning are in species in which young and old differ greatly in size, mobility, territoriality, or nutritional requirements, and such differences would obviously influence prey selection between age categories. Fledged birds, however, are generally equivalent to adults in size, mobility and food needs.

Differences in avian intraspecific food selection have not been widely documented. Newton (1967) discussed the phenomenon among species and between sexes in species of finches; in one case, a difference in bill length of 1mm

Table 1: Prey items eaten by migrating immature and adult Peregrine Falcons at Assateague Island, MD/VA, from 1970 through 1981. Totals for each category are shown as circled numbers.

	Number of selections by Peregrine Falcons			
	Immature		Adult	
Species	Female	Male	Female	Male
Flocking shorebirds				
Greater Yellowlegs (*Tringa melanoleuca*)			3	
Dunlin (*Calidris alpina*)			2	
Sanderling (*Calidris alba*)			2	
Semi-palmated Sandpiper (*Calidris pusilla*)	1		1	
Black-bellied Plover (*Pluvialis squatarola*)			1	
Purple Sandpiper (*Calidris maritima*)			1	
Long-billed Dowitcher (*Limnodromus scolopaceus*)	1			
Knot (*Calidris canutus*)		1		
Western Sandpiper (*Calidris mauri*)		1		
Pectoral Sandpiper (*Calidris melanotos*)		1 (5)	(10)	
All other birds		(81)	(12)	
Common Flicker (*Colaptes auratus*)	26	6	3	
Brown Thrasher (*Toxostoma rufum*)	5	1	3	
Mourning Dove (*Zenaid macroura*)	7			1
Green-winged Teal (*Anas crecca carolinensis*)	4		1	
Woodcock (*Scolopax minor*)	3	1		
Eastern Meadowlark (*Sturnella magna*)	2	2		
Yellow-billed Cuckoo (*Coccyzus americanus*)	2	1		
Rufous-sided Towhee (*Pipilo erythrophthalmus*)	2	1		
Gray Catbird (*Dumetella carolinensis*)	2			
Brown Creeper (*Certhia familiaris*)	1	1		
Tree Swallow (*Tachycineta bicolor*)	1	1		
Black-billed Cuckoo (*Coccyzus erythrophthalmus*)	1		1	
Swainson's Thrush (*Catharus ustulatus*)	1			
American Wigeon (*Anas americana*)	1			
American Robin (*Turdus migratorius*)	1			
European Starling (*Sturnus vulgaris*)	1			
Black Skimmer (*Rynchops niger*)	1			
Rock Dove (*Columba livia*)	1			
Yellow-bellied Sapsucker (*Sphyrapicus varius*)	1			
White-throated Sparrow (*Zonotrichia albicollis*)	1			
Winter Wren (*Troglodytes troglodytes*)		1		
Goldfinch (*Carduelis tristis*)		1		
Red-eyed Vireo (*Vireo olivaceus*)		1		
Pintail (female) (*Anas acuta*)			1	
Yellow-rumped Warbler (*Dendroica coronata*)			1	
Northern (Baltimore) Oriole (*Icterus galbula*)				1

was related to a significant difference in diet between sexes. Sex differences in prey selection have also been reported for several species of raptors, in which females are markedly larger than males (Snyder & Wiley 1976).

This paper reports differences in prey selection between migrating adult and immature Peregrine Falcons (*Falco peregrinus*), and discusses possible reasons for the disparity.

METHODS

During annual autumn surveys on Assateague Island (a thin, 39-mile-long barrier island off the coast of Maryland and Virginia, U.S.A.) from 1970 to 1981 (Ward & Berry 1972), Peregrines were often seen on the beach eating prey. Using a

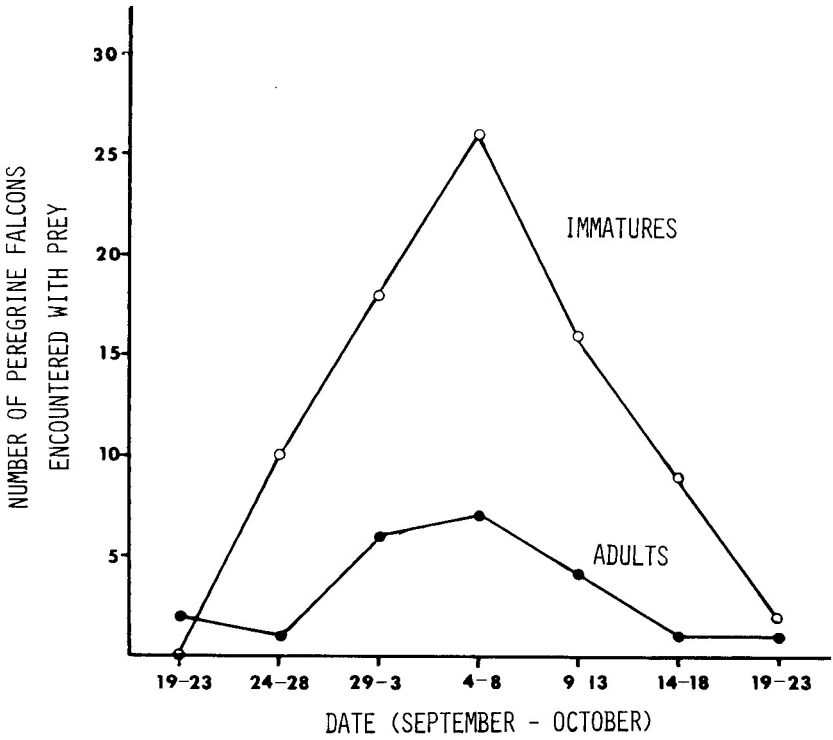

Figure 1: Dates when migrating adult and immature Peregrine Falcons were seen with avian prey at Assateague Island, MD/VA.

spotting scope, we determined the age (by plumage) and sex (by size) of each individual, and when it had finished eating, we collected prey feathers from the site for later identification in the laboratory. On a few occasions, prey feathers found encrusted to the feet or beak of a captured falcon were also collected. Prey species were identified by macroscopic and microscopic examination of the feathers and by comparison with study skins in the U.S. National Museum of Natural History, Smithsonian Institution, Washington, D.C.

RESULTS

Of 108 prey specimens identified during the 12-year survey, 86 were from immature Peregrines and 22 from adults. As collection and identification progressed through the years, we noticed that flocking shorebirds were captured more often by adult falcons than by immatures, whereas Common (Yellow-shafted) Flickers and other non-flocking birds were captured more often by immatures than by adults. (See *Table 1* for scientific names of all prey species.) Inspection of the data confirmed this difference: adult falcons selected about evenly from the two prey categories, but predation by immatures was heavily skewed away from flocking shorebirds (*Table 1*). The difference is significant statistically (Yates' corrected $Chi^2 = 21.42$, $p < 0.001$,1 df).

Both age classes captured prey on Assateague Island at about the same time of year (*Figure 1*), so seasonal differences in prey availability could not explain the

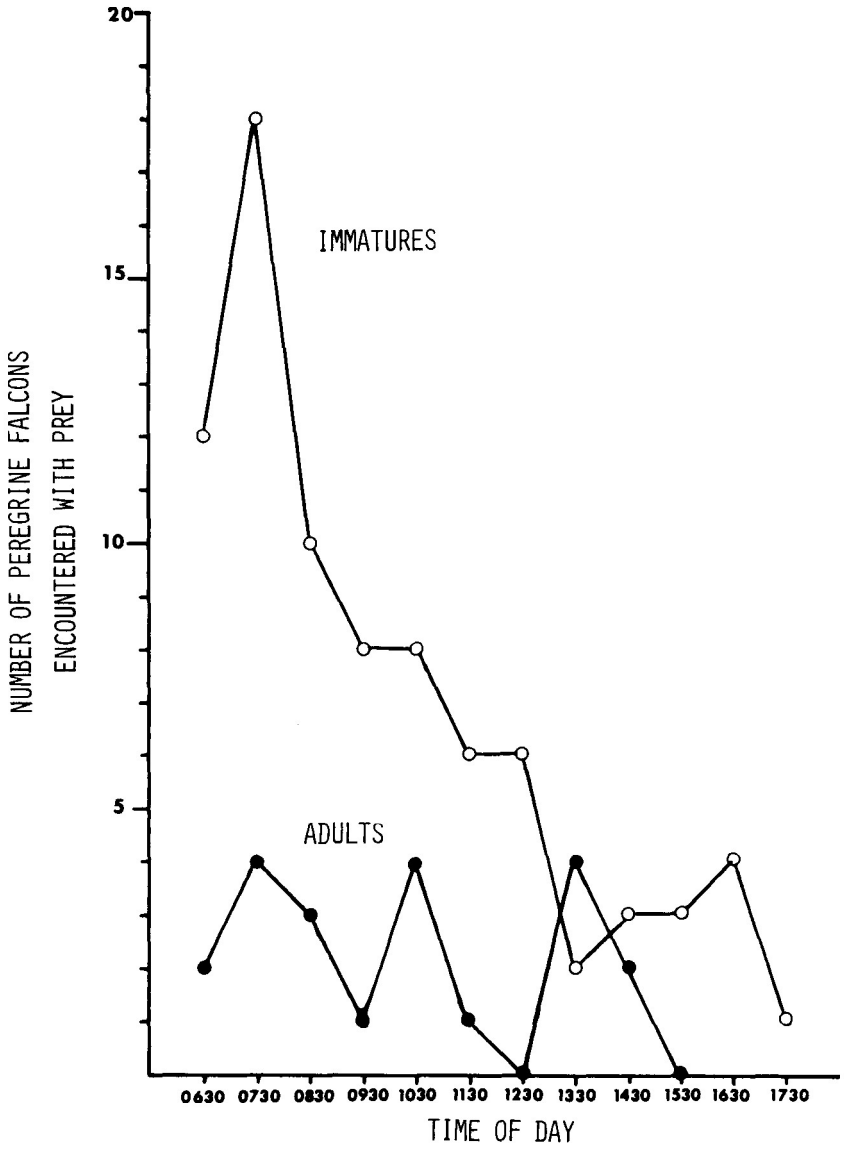

Figure 2: Times of day when migrating adult and immature Peregrine Falcons were seen with avian prey at Assateague Island, MD/VA.

differences in prey use. However, immatures were seen with prey mainly early in the day, declining later, whereas adults were seen at various times, with no obvious diurnal pattern (*Figure 2*). This apparent difference in timing of hunting activity could account for some of the disparity in prey species between age groups.

Table 2: Measurements of Arctic Peregrine Falcons (*Falco peregrinus tundrius*). From White (1968).

	Mean wing chord (mm)	Mean tail length (mm)	Mean weight (gm)
Adult male	308.3 (n = 64)	140.5 (n = 64)	610.9 (n = 12)
Immature male	311.1 (n = 27)	151.8 (n = 27)	570.0 (n = 4)
Adult female	351.8 (n = 62)	167.8 (n = 62)	952.0 (n = 19)
Immature female	349.6 (n = 30)	175.6 (n = 30)	889.0 (n = 3)

DISCUSSION

Our initial impulse was to conclude that flickers (which comprised 32 of 86 total captures by immatures) and other nonflocking birds must be easy prey for inexperienced juveniles. However, if flickers are easily captured, why do adult falcons not select more from this group? One reason may be the aerodynamic differences which exist between immature and adult Peregrines. Immatures have longer tails, broader (not longer) wings, and weigh less than adults (*Table 2*, from White 1968). As a result of the greater surface area and lower weight of an immature, wing loading increases as a Peregrine matures.

Similar aerodynamic differences have been described in Goshawks (*Accipiter gentilis*) (Mueller *et al.* 1976). Adults, with heavy wing loading, have a higher stalling speed and must fly more rapidly to remain airborne; but because of increased weight and flight speed, they have a greater impact than immatures when striking prey. If increase in weight from immature to adult is due primarily to an increase in the size of the flight musculature, then adults would also have greater acceleration. The authors concluded that the adaptive value of lighter wing loading in immatures was an increased manoeuverability, easier utilization of updrafts on migration, and a general reduction in the energy costs of flight (thus an easier migration and reduced need for food).

Immature Peregrines are therefore somewhat analogous to crop-dusting aircraft (great lift, manoeuverability at low speeds, low-energy flight), and adults to swept-wing jets (great acceleration, fast flight, high energy expenditure, little manoeuverability). The configuration and aerodynamic characteristics of immatures appear to be adaptations to enhance survival chances during the first year, including the first long migration from the Arctic to Latin America. Therefore flight characteristics of both age groups might well be manifested in the types of avian prey that young and old falcons are best able to pursue and catch.

Similar differences as those that exist between young and adults of one race of Peregrines may also occur in different races. In discussing differences in wing loading between the highly migratory subspecies *F. p. tundrius* and the less migratory *F. p. anatum*, White (1968) wrote: 'The ratio of wing to individual primary length (numbers 10 to 5) tends to indicate that *tundrius* has slightly longer primary feathers than *anatum*. . . . This difference may not prove to be statistically significant, but may nonetheless be a reflection of the migratory habits of *tundrius*'.

Evasive strategies of potential prey also influence capture success. All Peregrine hunting forays and prey captures observed at Assateague Island were in open areas, i.e. over the beach, wash flats, mud flats, bay and ocean. Of the major prey items, shorebirds congregated to feed in intertidal zones of ocean and bay. Flickers, thrashers, towhees, thrushes and cuckoos were often seen migrating solitarily onto the island from over the ocean, especially after passage of a cold

front. Most of the other species often migrated alone (except for tree swallows in loose groups and ducks in formation) across large, flat areas.

The protective strategy of a shorebird flock under attack by an aerial predator is to coalesce the group, to close ranks, so that the falcon would risk injury in a headlong dash through the tight formation. Etkin (1964) stated: 'Group formation, as in close flocking in birds, is so effective in protecting the individual that, generally speaking, predators try to isolate an animal from a group before attacking it. . . .' Immature Peregrines probably have neither the speed nor the experience necessary to separate a shorebird from a flock and attack it. A wheeling, undulating mass of shorebirds is likely to be a confounding target for a young falcon. Yet the factors above do not explain why adults do not prey more heavily on the large numbers of solitary migrants available.

Tinbergen (1960) reported that tits (Paridae) tend to choose a disproportionately high percentage of a certain type of larval Lepidoptera, and suggested that the birds were purposefully searching for this prey-type while largely ignoring other potential prey. He called this phenomenon a 'specific searching image' (SSI). Mook *et al.* (1960) provided additional evidence for SSI's in tits. For birds of prey, Snyder & Wiley (1976) suggested that '. . . the specific experiences of a given hawk in maturation may lead to a more or less distinctive prey preference'. After a series of laboratory experiments, Mueller (1968, 1971, 1974, 1975) concluded that development of the SSI was the most important factor influencing selection of white versus grey mice by American Kestrels (*Falco sparverius*). Conspicuousness of prey items seemed to be unimportant in Mueller's experiments, but several of his laboratory birds showed definite tendencies to select odd prey.

The formation of search images increases a predator's efficiency in locating and attacking prey (Ricklefs 1973). It would be to the advantage of a Peregrine to specialize, to develop an attack strategy for use on a common and abundant class of prey. It would be disadvantageous (in terms of energy expenditure and thus survival) to attack all manner of potential prey, i.e., flocking versus solitary fliers, large versus small birds, fast versus slow, those that evade by diving into the water or forest canopy versus those that try to outfly the falcon. Any falcon that attacked such a wide range of prey would probably be unable to perfect its technique for any one type, and would thus be at a disadvantage in the long run. Search images take time and positive reinforcement to form. Shorebirds are available to most Peregrines throughout the annual cycle, and shorebirds are quite vulnerable in that they occupy open habitats which generally offer no escape avenues other than flight. We suggest that adult Peregrines develop SSI's for shorebirds via repeated encounters, then '. . . perform a highly selective sieving operation on the visual stimuli reaching their retina' (Tinbergen 1960), while tending to ignore other potential prey when hungry. However, probably not all adult falcons form exclusive search images for shorebirds because some Peregrines that nest in the Arctic interior prey on passerines during the summer.

A strict diet of shorebirds might also produce nutritional deficiencies. Indeed, thiamine deficiency (Ward 1971) is one of the most common nutritional disorders in captive birds of prey. Virtually the only natural sources of thiamine for wild Peregrines are the germ and seed-coats of grains in the gut contents of seed-eating prey. Thus even adult Peregrines with strong SSI's for shorebirds might opt on occasion for granivorous prey. Of the adult's non-shorebird prey in this study, only the Black-billed Cuckoo is a total carnivore. Most of the remaining species subsist in autumn largely on vegetable matter, primarily seeds (C. S. Robbins, pers. comm.). Teal and Pintail, for example, eat mostly seeds of bulrushes (*Scirpus* sp.), plus other seeds and some leaf material. Mourning Doves subsist

entirely on seeds and a few berries, while about 80 percent of a Brown Thrasher's diet and 65 percent of a Yellow-rumped Warbler's diet in autumn are seeds and berries. Few data are available on the migratory food habits of the Northern Oriole; about 20 percent of its diet in summer is vegetable matter, and this figure is probably higher in autumn. In contrast, Common Flickers are insect-eaters. Adult Peregrines might tend not to subsist on them because of thiamine (or other nutritional) inadequacies in flicker tissues.

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