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CHAPTER 7

AGE-SPECIFIC FORAGING PROFICIENCY IN BIRDS

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1. INTRODUCTION

The fact that most birds exhibit high mortality during the juvenile period (Lack, 1954) suggests that this is a critical time in their life history. Much juvenile mortality may be attributed to a lack of proficiency in some aspects of behavior. For instance, juveniles must acquire skills in predator avoidance, foraging, and social interaction, particularly with competitors (Brown, 1975; Galef, 1976; Slater, 1983). Furthermore, they must learn to efficiently allocate time and energy to these activities so as to balance conflicting demands in reducing their vulnerability to both predation and starvation (Weathers and Sullivan, 1989). Thus the rate at which these behaviors develop is critical to the survival of juveniles and has implications for a variety of avian life history traits, particularly the extent of parental care (Ashmole and Tovar, 1968) and delayed maturation (Lack, 1968).

This chapter focuses on the factors which influence juvenile foraging skills, particularly the constraints which prevent juveniles from rapidly acquiring adult levels of foraging proficiency. Periods of high mortality, such as the juvenile period, provide strong opportunities for

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the action of natural selection (Arnold and Wade, 1984). Yet, despite potentially high selection pressures on the rate of behavioral development, juvenile proficiency often lags behind that of adults for a considerable period of time. This suggests that the rate of behavioral development is constrained by one or more factors. The factors constraining development are of particular interest for understanding the evolution of behavioral or morphological traits (Maynard Smith *et al.*, 1985; Irwin, 1988). It has been argued that more attention should be paid to the development of foraging skills, since this may be when selection acts more strongly on foraging performance (Zach and Smith, 1981).

Whereas the factors influencing behavioral ontogeny can conveniently be divided into internal and external factors, understanding their interaction and influence on behavior can be difficult (e.g., Hailman, 1967; S. M. Smith, 1983). For example, during the ontogeny of foraging behavior, improvements in foraging skills might be attributed to maturation of the nervous and muscular systems as well as learning (e.g., Cruze, 1935). Learning can improve a predator's ability to locate and identify appropriate prey (e.g., Kamil and Yoerg, 1982; Shettleworth, 1984), and also contribute to improved neuromuscular coordination necessary for prey capture or handling. These factors all depend on at least some level of interaction with the environment. For instance, the physical environment, such as light levels or weather conditions, can influence foraging proficiency of the young (e.g., Carl, 1987). The biotic environment, such as the distribution and abundance of prey, can also affect the efficiency with which the young forage (e.g., Sutherland *et al.*, 1986). Social factors, such as observational learning and local enhancement from experienced adults, further contribute to the improvement of juvenile foraging skills (e.g., Palameta and Lefebvre, 1985) in contrast to aggression from dominant adults which can hinder juvenile foraging proficiency (e.g., Goss-Custard *et al.*, 1987a, b, c). The identification of these factors, their mode of interaction, and assessment of their relative importance during the development of behavior is the goal of those studying behavioral ontogeny, and is the approach taken in this chapter.

This review does not attempt to examine the ontogeny of foraging through all phases of development, but rather is limited to the period when the young are capable of feeding independently and are free from all parental care. At this time the juveniles are free-flying and have obtained most of the morphological and physiological traits of the parents. During this stage most morphological growth is complete and the juveniles have usually obtained a mass equivalent to that of a mature adult, yet their feeding skills are not equivalent to those of other adults. The weakness of this approach is that it ignores the early stages of behavioral development upon which a juvenile bird's later foraging

proficiency might depend. That early developmental stages are important was emphasized by Hailman (1982) who notes that the current behavioral phenotype of an organism is dependent upon previous behavioral phenotypes as well as their interaction with the genotype and environment. Although not as thoroughly examined, reference will be made therefore to appropriate studies on earlier stages of development. Throughout this review, I use the term juvenile to indicate young individuals who have not reached sexual maturity. Thus, juvenile passerines are individuals in their first year of life whereas juvenile nonpasserines may be in their first, second, or third year (e.g., gulls).

If juveniles are less proficient foragers than adults they may compensate in a variety of ways—the most obvious is by foraging longer. Juveniles might also forage in different habitats or patches, use different search patterns, consume different sizes or types of food, or steal from more adept foragers. The compensation options available to juvenile foragers are of considerable interest in light of recent theoretical work on the alternative strategies applied to individual differences in behavior (e.g., Maynard Smith, 1982; Partridge and Green, 1985).

One valuable theoretical approach to foraging behavior is to assume that foragers make a series of hierarchical decisions (Gass and Montogomerie, 1981; Orians, 1981). This hierarchical decisionmaking process is initiated when a forager selects a general habitat in which to feed. Next, it selects a patch in which to feed. Once in a patch the forager must choose a particular search pattern, followed by a decision as to which food items to consume. In some instances, a decision is required as to which capture technique is to be used to subdue the prey. Finally, for certain food types, the forager must choose a method for handling the food as it is consumed. This hierarchical approach to studying foraging behavior has proven useful and is fundamental to the organization of optimal foraging theory (see reviews in Krebs *et al.*, 1983; Krebs and McCleery, 1984; Pyke, 1984). Age-related differences can occur in each of these foraging stages due to a young bird's lack of proficiency in a specific stage and/or because the young forager compensates for its lack of skills at another stage.

Thus this review focuses on the mechanics of juvenile foraging proficiency in an effort to:

1. Identify the specific stage or stages during foraging which account for the reduced foraging proficiency of juveniles relative to adults during a typical foraging sequence (i.e., the progression involving foraging site, search patterns, diet choice, prey capture, and prey handling).
2. Determine the factor or factors which constrain juvenile forag-

ing proficiency (i.e., maturation, learning, adult dominance, and predation).

3. Determine how juveniles compensate for their lack of foraging proficiency (i.e., more time feeding, searching in different habitats, selecting different prey, relying on observational learning, and piracy).

2. THE NATURE OF THE LITERATURE

This review is based on a relatively specialized literature that is subject to certain characteristics and limitations. The review is of studies in which the foraging behavior of self-feeding young (juveniles) is compared to that of older individuals (adults), as summarized in Section 6. The predominant interest of this literature, at least in its earliest years, has been to document age-related differences in foraging proficiency in support of Lack's (1968) delayed breeding hypothesis (e.g., Orians, 1969; Recher and Recher, 1969). Thus much of the initial focus was to simply demonstrate that juveniles were more inept foragers than adults, rather than uncover how, where, and why juveniles were less proficient. A few studies on the ontogeny of foraging behavior have also contributed to this subject by identifying factors controlling foraging development (e.g., Norton-Griffiths, 1967, 1968, 1969). Only recently have workers tried to identify how juvenile foragers differ from adults, determine the consequences for juveniles, and uncover how juveniles compensate for their less efficient foraging abilities (e.g., Goss-Custard *et al.*, 1982a, b, c; Goss-Custard and Durell, 1983, 1987a, b, c).

Age-related differences have usually been quantified in three different ways: foraging success (number of prey items captured per capture attempt); foraging rate (number of prey items captured per unit time); and interfood time interval (time interval between capture of one prey item and the next). Each of these measures incorporates different components of the foraging sequence. Foraging success measures the ability to capture prey once it has been located; it includes the ability to recognize and select capturable prey as well as capture ability, but it does not include searching or handling abilities. Foraging rate and interfood time interval both quantify search, recognition, selection, capture, and handling abilities together. Unfortunately, these measures do not allow quantification of proficiency at each individual stage of a foraging sequence (i.e., search only, recognition only, etc.). Therefore, some workers have measured time used in each stage (e.g., search time, handling time, etc.) to quantify age differences (Sutherland *et al.*, 1986).

However, most studies have not identified either at what stage of the foraging sequence age-related foraging differences are greatest or the relative rates of development of foraging abilities.

Approximately 90% of the field studies on age-related foraging proficiency have not involved color-banded individuals so that the actual rate of development of foraging proficiency cannot be determined for most species. Although many workers have suggested that juvenile foraging improves with time, their observations are based on unbanded birds at different times of the year. Such apparent improvement might simply result from the interim mortality of less efficient individuals (cf. Orians, 1969). This explanation could also apply to those species in which different age classes can be distinguished on the basis of plumage (e.g., gulls) and in which workers have documented improved proficiency with advancing age class of unbanded birds. Thus in the absence of marked individuals it is difficult to determine at what age juvenile birds obtain adult levels of foraging proficiency and the rate of its development.

Although studies of age-related foraging proficiency have been made with a variety of species, they do not accurately represent the diversity of avian taxa and the full spectrum of foraging methods (Section 6). For instance, aquatic species are well represented with studies of 26 species of Charadriiformes, six species of Ciconiiformes, three species of Pelecaniformes, two species of Gruiformes, and one species of Falconiformes. Most of the aquatic species fed primarily or partially on fish (62% of aquatic species), and their most frequent hunting technique, plunge diving, was studied in pelicans, Ospreys (*Pandion haliaetus*), gulls, and terns (16 studies). Gulls have been the most frequently studied group, in which 23 studies have documented age-related differences in a variety of foraging situations. The predominance of certain taxa and foraging modes in studies of age-related differences in foraging proficiency is undoubtedly due to the ease of observing foraging sequences and the presence of age-related plumage differences. For example, Falconiformes are poorly represented in published studies, most likely because of the difficulty of observing foraging sequences. Also, studies of age-related foraging differences in Passeriformes are underrepresented. Furthermore, many avian orders simply have not been studied for age-related foraging proficiency. Therefore in light of the skewed representation of avian taxa and foraging modes, caution must be exercised in developing generalities regarding age differences in avian foraging proficiency. Nonetheless, the available studies demonstrating that juveniles are less proficient foragers than adults, regardless of diet, supports the view that this is a general phenomenon.

The rates at which juveniles obtain adult levels of proficiency, however, varies widely.

3. FORAGING COMPONENTS

3.1. Foraging Site

Habitat selection in birds has been relatively well studied (for a recent review see Cody, 1985). While relatively few studies have focused on the ontogeny of habitat preferences, their results demonstrate that the development of habitat preferences involves a complex interaction of a diversity of internal and external factors, such as genetic predispositions, sensory physiology, imprinting, associative or trial-and-error learning, and social interactions (reviewed in Klopfer and Ganzhorn, 1985). Juveniles are often less specific in their habitat preferences than older birds (Bairlein, 1981) suggesting that experience (Partridge, 1979) or other factors influence their later choices. The development of foraging site preferences specifically has been found to involve a complex interaction of innate bias, exploration, and learning (Greenberg, 1984, 1987).

The selection of a habitat is one of the first decisions faced by a forager followed by the selection of a patch or patches in which to feed. However, what constitutes a habitat or a patch will vary from species to species, and the effective size of a habitat or patch will vary with the size and mobility of a forager. Therefore the problem of defining either a habitat or a patch is a problem of ecological grain, which often cannot be easily divided into a simple dichotomy (Emlen, 1973). Many of the workers studying age-related differences in foraging seem to have used the term "habitat" or "patch" indiscriminately. Because of the difficulty of distinguishing between habitat and patch selection by foragers, I will focus this discussion primarily on patch selection with occassional reference to habitat selection studies. Although adults and juveniles might frequently use different habitats, the factors responsible for age-related differences in habitat use are frequently the same as those accounting for age-related differences in patch use.

Most studies of patch selection assume that a forager's decisions are based on the energetic return realized from feeding in a patch per unit effort (e.g., Royama, 1970; MacArthur, 1972; Pyke *et al.*, 1977; Krebs and McCleary, 1984). Although, other factors, such as nutrition, competition, and predation may interfere with this scheme (e.g., Werner, 1976; Clark, 1980), the majority of studies indicate that adult

foragers attempt to feed in the most profitable patches available (e.g., Royama, 1970; Smith and Dawkins, 1971; Smith and Sweatman, 1974; Wakeley, 1978; Pulliam, 1980). This might also be true for juveniles, although a variety of factors might limit their use of the most profitable patches.

Studies on species as varied as pelicans, cormorants, oystercatchers, gulls, herons, ospreys, kites, parrots, titmice, and warblers have found age-related differences in habitat or patch use (e.g., Moyle, 1966; Ficken and Ficken, 1967; Howe, 1974; Davis, 1975; Morrison *et al.*, 1978; Goss-Custard *et al.*, 1982b; Burger and Gochfeld, 1983; Brandt, 1984; Goss-Custard and Durell, 1983; Bourne, 1985; Draulins and Van Vessem, 1985; Magrath and Lill, 1985; Maccarone, 1987; Goss-Custard and Durell, 1987a, b, c; Gustafsson, 1988; East, 1988; Edwards, 1988, 1989b; Hesp and Barnard, 1989). These studies have suggested several explanations which might account for age-related differences in foraging sites, such as: (1) competition in which dominant adults displace juveniles from certain foraging sites; (2) inability of juveniles to accurately evaluate patch differences; (3) diet differences arising from lack of juvenile proficiency for searching, capturing or handling prey; and (4) different nutritional requirements. Explanations 1 and 2 represent developmental constraints in which juveniles have not yet obtained adult levels of proficiency and generally decrease survival of juvenile birds. Explanations 3 and 4 generally have a positive effect on juvenile survival in that they compensate for a lack of juvenile skills or provide certain nutrients. It is conceivable that more than one factor might be responsible for a species' age differences.

Competition in which dominant adults displace subordinate juveniles from the most profitable patches is the most frequently cited reason for age-related differences in foraging site use. For example, Glaucous-winged Gulls (*Larus glaucescens*) in immature plumage were forced by aggressive adults to feed in suboptimal habitats while foraging along a salmon stream (Moyle, 1966). During a two year study, Maccarone (1987) found that adult and juvenile European Starlings (*Sturnus vulgaris*) used available foraging substrates differently. Adults were more numerous than expected in managed grassland both years, and they were more abundant than expected at human-assisted food sources in one year. Adult aggression often prevented juveniles from using these habitats. Juveniles were more numerous in unmanaged grassland and in soybean and wheat fields both years, and in agricultural fields other than soybean and wheat in one year. Maccarone suggested that juveniles might reduce competition with adults on managed grassland by using agricultural fields and unmanaged grassland,

in which adults were less common. Another example occurs in Coal Tits (*Parus ater*) on the Baltic island of Gotland where juveniles are more generalized foragers than adults as illustrated by their tendency to forage on both the outer and inner parts of trees, whereas adults use the central part. Gustafsson (1988) attributed this difference to adult competition for food and noted that as juveniles became older they shifted their foraging to the central parts of the tree. A similar difference between adult and juvenile Willow Tits (*P. atricapillus*) was found by Ekman and Askenmo (1984) who attributed it to dominant adults trying to avoid predators rather than a response to food supplies. Ekman (1987) notes that these two explanations are not mutually exclusive, because foraging in a safe locale will reduce vigilance thereby allowing more time for feeding. In another case, Magrath and Lill (1985) noted that since juvenile Crimson Rosellas (*Platycercus elegans*) were behaviorally subordinate to adults at artificial feeding stations, juveniles may be excluded from the best habitat and thus have to spend more time feeding than adults.

Frequently, it is both the subordinate status of young birds and their lack of foraging proficiency which results in differential patch use. Unfortunately, it is often difficult to disentangle the separate effects of foraging skill and interference on the intake rate of young birds (Draulines and Van Vessem, 1985; East, 1988). However, this was achieved by Goss-Custard and his associates in a detailed series of studies on the interaction of aggression and juvenile foraging proficiency in different patches or habitats by Eurasian Oystercatchers (*Haematopus ostralegus*) (Goss-Custard *et al.*, 1982a, b; Goss-Custard and Durell, 1983; Goss-Custard and Durell, 1987a, b, c). Their work with color-banded birds nicely demonstrated that adults (> 4 years of age) displaced immatures (2–4 years of age) from the preferred mussel beds. When adults were present, the immatures moved to low ranked beds and had a tendency to change mussel beds more frequently than adults. However, once the adults left in the spring to breed, immatures foraged in the high ranked mussel beds, until the adults returned and displaced them again in the autumn. As the birds matured, the mean rank of the bed on which they fed in winter increased, while their status and competitive ability increased. Most adults seen at least five times in one year occurred on only one habitat and ate only one kind of prey. In contrast, immature birds were often seen on two or three habitats, and consumed two prey species more often than one. At high water, immatures occurred more frequently than adults in fields and foraged on more easily obtainable prey. Immature oystercatchers forag-

ing in fields during mild winters have greater mortality because of accidents and a wider array of parasites, while during cold winters the fields are unavailable to them. All these factors contributed to the higher mortality rates of the younger birds (Heppleston, 1971; Goss-Custard *et al.*, 1982c).

It is apparent from the studies on age-related differences in patch or habitat use, where competition is believed to be important, that adult aggression may force juveniles into suboptimal habitats and/or require juveniles to feed in a wider range of foraging sites, both of which could require juveniles to feed on different prey types. By forcing juveniles into suboptimal patches, adults may retard the rate at which juveniles obtain foraging proficiency on the most profitable prey types. This may be the case in immature Eurasian Oystercatchers which begin to eat mussels only when they are mature enough to compete with adults on the mussel beds (Goss-Custard and Durell, 1983).

Under certain conditions, juveniles may compensate for their lack of skill in finding, capturing, or handling prey by feeding in sites where their lack of skill is less likely to hinder them, while older birds forage in sites requiring more skill. For instance, young gulls often congregate on dumps, presumably because food is either easier to find or capture than when using more traditional sites, which may require learning and practice (Schreiber, 1968; Spaans, 1971; Cooke and Ross, 1972). The higher proportion of juvenile European Starlings feeding in cherry orchards has been attributed to their preference for cherries as a result of their inability to capture the larger insects preferred by adults feeding elsewhere (Stevens, 1985). Juvenile Olivaceous Cormorants (*Phalacrocorax olivaceus*) had higher prey capture rates in an area where juveniles outnumbered adults than in an area where adults were more numerous, suggesting that juveniles hunted in areas where they were most successful (Morrison *et al.*, 1978). Burger and Gochfeld (1983) found that young Laughing Gulls (*Larus atricilla*) concentrated their feeding in areas where the foraging task was easiest and where their feeding success approached that of adults. In habitats where food was readily available (e.g., garbage and fish offal) the differences between age classes in foraging success was negligible. Thus it appears that young Laughing Gulls compensate for their less developed foraging skills by concentrating their foraging in specific areas. In Brown Pelicans (*Pelecanus occidentalis*), prey density had the largest effect on patch use by both adults and juveniles (Brandt, 1984). However, diving proficiency (success rate) had the least influence on adult patch use, since adult diving proficiency varied little between patches. In con-

trast, juvenile diving proficiency was quite variable between patches and thus together with prey density had a strong effect upon juvenile patch use.

Another example of age-related differences in patch use resulting from compensatory site selection by unskilled juvenile foragers has been described by Hesp and Barnard (1989). They found that young Common Black-headed Gulls (*Larus ridibundus*) were less effective at stealing earthworms from Northern Lapwings (*Vanellus vanellus*) than were adults, and predicted that juveniles should opt for alternatives to kleptoparasitism when their efficiency at the latter is low and if alternatives offer potentially greater intake rates. As predicted, they found a higher proportion of juveniles on plowed or stubble fields and in flocks following plows than in flocks ("patches") of lapwings. Also, adults were more abundant in high density lapwing flocks than low density flocks, where juveniles were occasionally found. Presumably because juveniles lacked many of the skills of adults in kleptoparasitism, they were proportionately less abundant in lapwing flocks and more abundant in plowed/stubble fields. This is consistent with the hypothesis that juveniles are selecting the most profitable patches in relation to their foraging proficiency.

The last factor which can explain age-related differences in patch use results from the inability of juveniles to discriminate between the most profitable patches utilized by adults. In this instance, juveniles cannot compensate for their lack of foraging abilities because they are unable to differentiate between patches. For example, Edwards (1988) showed that adult Ospreys foraging during the postfledgling period exhibited a statistical preference for the littoral habitat which had the greatest fish abundance, rather than the nearby limnetic habitat. In contrast, juveniles foraging at the same time did not display any habitat preference, but rather used littoral and limnetic habitats in relation to their availability, suggesting to Edwards (1989b) that juveniles had not yet obtained the ability to recognize habitat differences in prey abundance. Unfortunately, such demonstrations are unusual since very few studies have sampled the prey density or abundance in different patches while monitoring foraging by different age classes, and thus the current literature is inadequate to assess how often juveniles fail to accurately select the most profitable patches.

Although age-related differences in patch use by Brown Pelicans were found by Brandt (1984), none could be attributed to the inability of juveniles to select profitable patches. Both adults and juveniles were strongly influenced by the foraging efforts of the other; adults tended to join juveniles foraging in a patch and vice versa. Interestingly, this

attraction to other foragers (local enhancement) augmented the foraging success only of juveniles. In this case, local enhancement which contributed to juvenile diving success, may have been the factor allowing juveniles to achieve "adult" levels of patch selection proficiency. Porter and Sealy (1982) found that juvenile Glaucous-winged and California Gulls (*Larus californicus*) did not initiate feeding flocks, were less adept at finding food, and had a lower feeding success rate. One of the ways in which juveniles compensated for these inadequacies was by joining actively feeding groups of birds. In addition, juveniles were more likely than adults to approach gull models floating in a bay. Thus local enhancement may be one way in which juveniles compensate for their inability to select profitable patches.

It is important to note that age-related differences in habitat or patch use have not always been found, even when the birds showed age-related differences in foraging proficiency (Puttick, 1979; Gochfeld and Burger, 1984; Greig-Smith, 1985; Burger and Gochfeld, 1986; Bildstein, 1987). These studies suggest that specific, but as yet unidentified, conditions are necessary to permit differential habitat use by adults and juveniles.

Finally, although we can frequently document which habitats or patches are used by adult and juvenile foragers, no field workers have yet documented the search time necessary for a bird to locate these habitats or patches. Burger and Gochfeld (1983) noted this problem and recommended that "habitat search time" be added to Schoener's (1971) concept of "search time" to more accurately reflect the time a bird searches for a given food item. If and when "habitat search time" is measured in the field (possibly with radio telemetry?) it would seem likely that juveniles will be less proficient than adults.

3.2. Search Methods and Patterns

Both the pattern and method of searching by foragers in response to variation in resource density can affect net energy intake (e.g., Tinbergen *et al.*, 1967; Croze, 1970; Cody, 1971; J. N. M. Smith, 1974a, b; Charnov *et al.*, 1976). It should not be surprising that adults and juveniles differ in their search methods. Unfortunately quantification of seraching methods in the field is very difficult and only a few field studies have documented age-related differences. A common searching difference detected between adults and juveniles is in the speed with which foragers move through a patch. For example, adult American Robins (*Turdus migratorius*) tend to search more slowly (steps/min and steps/bout) and cover less area than do juveniles, but as a consequence

are more successful than juveniles (Gochfeld and Burger, 1984). Similarly, adult (> 2 years) Herring Gulls (*Larus argentatus*) tend to walk more slowly than the less successful first and second year gulls foraging in a dump (Greig *et al.* 1983). Verbeek (1977a) also noted that adults remove more objects in their search for food in dumps and commented that juvenile gulls may find it easier to steal because they have not yet learned to dig by removing objects. However, in some instances juveniles appear to put more time and effort into the searching, such as in Northwestern Crows (*Corvus caurinus*) in which juveniles spend more time searching for clams in mud banks than do adults (Richardson and Verbeek, 1987).

One of the few studies to quantify differences in search patterns is that of Wunderle and Lodge (1988), which compared the foraging abilities of naive, hand-reared juvenile Bananaquits (*Coereba flaveola*) to those of captive wild adults foraging. The artificial patch contained a random array of either open or closed flowers. Foragers removed the tops from covered flowers in order to feed, thereby marking all visited flowers. Open flowers provided no clues as to previous visitation. Adults searched the patch more thoroughly and made fewer flower revisits during each foraging bout than did juveniles. Flower revisitations, within a foraging bout, by juveniles were more than expected by change while those made by adults were fewer than expected by chance. This was true for both open and covered flower types. The increase in foraging proficiency with age involved several different characteristics. On open flowers, adults and juveniles differed in the frequency of their patch departures and returns, and in their pattern of turning in the patch, thus resulting in a more complete search of the patch by adults. On covered flowers, however, the two age classes differed primarily in their pattern of turning, and adults made a more complete search of the patch. Both age classes used the presence or absence of flower covers as a clue to previous visitation. It is likely that adults use their memory to reduce their chance of revisiting flowers during a foraging sequence. The importance of memory is suggested by the departures of adults from depleted areas of the patch and their movement to unvisited areas when they foraged on open flowers (i.e., flowers with no clues indicating previous visitation). It is likely that a particular pattern of the random array of flowers in one section of the patch is remembered by the departing adult and thus avoided on its return. With experience, juveniles may associate memory and avoidance of previously visited flowers with increased energy intake per foraging effort. Thus young Bananaquits may improve their searching

abilities by learning to use their memory by a trial-and-error process to reduce flower revisitations.

Recent studies on search strategies and spatial learning have indicated that different species may show either a preference for locations where they have just found food (win-stay) or avoidance of those locations (win-shift). A major factor influencing win-shift or win-stay learning may be whether the resource is depleted on a single visit (Olton *et al.*, 1981). For example, if a food resource is easily depleted during a single visit, a forager would do best to shift to another locality rather than revisit the original site. This win-shift pattern is common among adult nectarivores, which rarely revisit flowers during a foraging bout (Gill and Wolf, 1977; Kamil, 1978). However, if the food resource is not exhausted during a visit it would be advantageous for the forager to return to the same location to feed. The win-stay pattern has been found to occur in titmice (*Parus* sp., Smith and Sweatman, 1974) and adult Red-winged Blackbirds (*Agelaius phoeniceus*, Beauchamp *et al.*, 1987).

Laboratory studies have demonstrated an age-related effect in controlling the relative balance of win-stay and win-shift responses, which can influence the foraging proficiency of juveniles. For example, Beauchamp *et al.* (1987) conducted experiments with Red-winged Blackbirds in a three-choice maze, where individual foragers were allowed to either consume all the food from the first visited site (depletion condition) or only some of it (non-depletion condition). After a bird's first choice, it was subsequently re-tested to determine if it returned to the previously visited site (win-stay) or whether it chose an alternate site (win-shift). Under the depletion condition, both adults and juveniles were more likely to show the win-shift response. However, under the non-depletion condition adults showed a win-stay response in contrast to juveniles which responded randomly. Thus in this case juvenile blackbirds must learn the win-stay response to efficiently feed in non-depleting patches.

In contrast, juveniles of the nectarivorous Bananaquit must learn the win-shift response to prevent revisitation to recently emptied flowers (Wunderle and Soto-Martinez, 1987). Laboratory experiments with artificial flowers demonstrated that wild-caught adults were quick to learn win-shift tasks, but had difficulty learning to return to flowers in a position just visited (win-stay). However, naive juveniles learned win-shift and win-stay problems with equal facility. This juvenile learning flexibility (i.e., no predetermined win-shift response) may account for their relatively high level of flower revisitations, which re-

duces their foraging efficiency (Wunderle and O'Brien, 1985; Wunderle and Lodge, 1988).

In summary, only a few lab studies have examined adult-juvenile differences in searching behavior in detail, while some field studies suggest that differences exist. Obviously, age-related differences in search behavior should be studied for more species before conclusions can be made regarding the factors controlling and constraining the development of this behavior. However, the existing evidence suggests that some of the important factors in the development of searching behavior are learning via association and trial-and-error.

3.3. Food Recognition and Selection

The development of food recognition by young birds involves an intricate interplay of learning with genetic predispositions. During normal development young birds initially show curiosity and exploratory behavior by pecking at both appropriate and inappropriate items, but with time concentrate their pecking on edible items (e.g., Hogan-Warburg and Hogan, 1981; Davies and Green, 1976; Moreno 1984). Trial-and-error plays an important role in the development of food recognition with a complex interaction between avoidance and acceptance learning, as elegantly demonstrated by experimentation with domestic chicks (e.g., Hogan, 1973a, b, 1977a, b; Hale and Green 1979, 1988).

Mueller (1974) summarized the theories concerning prey recognition in birds and mentioned three hypotheses: (1) juvenile learning is from their parents; (2) juvenile learning is from personal experience; (3) juvenile learning is mostly independent of personal experience and is thus primarily genetically based. Each of these hypotheses is likely to be correct depending upon the species (S. M. Smith, 1983). For example, learning from the parents and personal experience is probably important for many precocial species (e.g., Turner, 1964). While for other species such as American Kestrels (*Falco sparverius*) and Loggerhead Shrikes (*Lanius ludovicianus*), parental teaching is likely to be unimportant (Mueller, 1974; S. M. Smith, 1972, 1973). S. M. Smith (1983) notes that for a variety of species there is strong evidence for a genetic basis in the development of food recognition, which may allow for its rapid development.

After the young have achieved independence from their parents, age-related differences may occur in prey recognition and selection producing differences in diet. These two stages of foraging can differ with age because: (1) juveniles are less proficient than adults at prey recognition and selection; (2) juveniles are less skilled at another forag-

ing stage (i.e., capture or handling) and thus compensate by selecting a diet different than that utilized by adults; (3) juveniles have different nutrient requirements than adults (e.g., Savory, 1977; Stokkan and Steen, 1980); (4) adult dominance influences juvenile diet selection by preventing juveniles from selecting the most profitable prey types (e.g., Goss-Custard and Durell, 1983; Amat and Aguilera, 1990). This discussion will focus primarily on the age-related proficiency differences (1 and 2 above) in prey recognition and selection when adults and juveniles are foraging in the same locality. Cases of age-related diet differences arising from differences in foraging site were discussed previously.

Juveniles may be less proficient at recognizing suitable prey, as a result of their inexperience. For example, Mueller and Berger (1970) found that traps baited with sparrows captured more adult Sharp-shinned Hawks (*Accipiter striatus*) than juveniles, while traps baited with pigeons took more juveniles than adults. Mueller and Berger concluded that the adult Sharp-shinned Hawks were less likely to attack inappropriately large prey than were juveniles. Juvenile Royal Terns (*Sterna maxima*) were more likely to be caught on fishooks than were adults whose ability to recognize capturable prey was an important factor in their fishing success (Buckley and Buckley, 1974). Although naive Pinyon Jays (*Gymnorhinus cyanocephalus*) showed an immediate preference for pinyon seeds over other objects, their ability to distinguish between good and bad seeds (endosperm absent) improved with learning (Ligon and Martin, 1974). Naive Red-winged Blackbirds attacked aposematically colored stinkbugs at the same rate as they attacked mealworms (Alcock, 1973). However, as the young blackbirds obtained experience with the distasteful stinkbugs they were less likely to attack them. This, of course, is an important assumption for the evolution of aposematic coloration and mimicry. Numerous studies have demonstrated that young birds learn to avoid unpalatable prey species, although some species appear to have inborn recognition of dangerous prey (for a review see S. M. Smith, 1983).

Inappropriate objects might also be attacked by young foragers, as demonstrated by juvenile Gray Herons (*Ardea cinerea*) which frequently seized inanimate objects (such as floating feathers and sticks), items adults rarely seized (Cook, 1978). Juvenile Green-backed Herons (*Butorides striatus*) used more inappropriate objects (plant material) while bait fishing than did adults which relied more on animal baits that were more effective at attracting fish (Higuchi, 1986). For kleptoparasites, recognition of an appropriate "victim" from which to steal probably requires experience which juveniles may lack. For example,

adult Laughing Gulls preferentially attacked juvenile pelicans, presumably because they were easier to exploit than adult pelicans, while yearling gulls showed no preference (Carroll and Cramer, 1985).

To accurately recognize prey, juvenile birds may need to develop search images (Dawkins, 1971), which may initially be imperfectly retained. This may occur in Black-winged Stilts (*Himantopus himantopus*) studied by Espin *et al.* (1983) who suggest that inaccurate prey recognition might contribute to the significantly higher number of intention movements made by juvenile stilts. In Royal Terns, juveniles repeatedly circled back and forth over an area, making many intention movements to dive and often abandoning dives close to the surface, behaviors rarely observed in adults (Buckley and Buckley, 1974). The higher incidence of intention movements by juveniles, suggesting imperfect search image formation, has also been found in several gull species (Porter and Sealy, 1982; MacLean, 1986).

Juveniles might compensate for their inability to accurately recognize suitable prey items by observing other foragers (Galef, 1976). This may take the form of social facilitation, in which one of the behaviors already in an animal's repertoire is released by the presence of another doing that behavior (Thorpe, 1963). Or, as discussed earlier, there may be local enhancement in which an individual is attracted to a novel environmental stimulus by the presence of another forager and then achieves a food-finding ability by individual learning (Thorpe, 1963). A naive observer copying an experienced individual's actions regardless of its outcome is "blind" imitation or "mindless" copying (Gould, 1982). Each of these phenomena could cause a naive forager to have a higher probability or rate of learning after witnessing an experienced forager. Furthermore, studies have demonstrated that naive birds will frequently adopt the diet of the experienced model (e.g., Klopfer, 1959; Murton, 1971; Partridge, 1976; Palameta and Lefebvre, 1985). In this way juveniles might quickly adopt the diets of adults (Richardson and Verbeek, 1987). Even interactions between naive siblings can result in diet similarities (Edwards, 1989b).

For a predator to select an optimal diet, it should rank prey types according to their profitability (energy yield per unit handling time) and their overall abundance. When the most profitable prey types are abundant the predator should specialize; as the abundance of the most profitable prey declines, the predator should generalize (for review see Pyke *et al.*, 1977). A variety of adult animals seem to fit the optimal diet model (for review see Krebs *et al.*, 1983) which depends on a predator's ability to access prey profitability and abundance.

It is presently difficult to determine when and how quickly juve-

niles can select an optimal diet. Some studies show that recently independent juveniles can select the most profitable prey types, within the limits imposed by their foraging inefficiency (Richardson and Verbeek, 1987; Sullivan, 1988b), and that juveniles can sometimes evaluate prey densities as well as can adults (Brandt, 1984). These results suggest that some juveniles, possibly at an early age, might have the ability to select an optimal diet. However, an inability to recognize appropriate prey, as discussed earlier, and a failure to respond to fluctuations in prey abundance (Edwards, 1989b) suggest that for other species the ability to select an optimal diet might require considerable time for development. Obviously more work is needed to determine when and how optimal diet selection arises in young birds.

Ineffective capture skills may cause juveniles to select different types or sizes of prey than those taken by adults. For example, inexperienced juveniles may feed on easily captured or found food items while more experienced adults capture more difficult prey. Stevens (1985) suggests that this may be the case in European Starlings, in which juvenile pecking success was 5.97% for large insects (mostly leatherjackets) compared to 48.1% success for adults, while the difference was considerably less when feeding on small insects. As expected, adults took large prey such as leatherjackets, which represented 82.2% of their diet (by dry weight) versus 34.9% taken by juveniles. However, juveniles pecked more at cherries on the ground and at insects in cow dung, which are easily accessible in comparison with leatherjackets. Stevens related this to the previous studies which indicated an extraordinary high proportion of juveniles in cherry orchards. Feare (1980) earlier suggested that different nutritional requirements could explain the preference of juveniles for cherries. Stevens (1985) argues that this nutrition hypothesis is unlikely because growing juveniles have high protein needs and do their best to gather animal food: juveniles did more searching for grubs than did adults and fed for longer time periods in a variety of locations where insects were easier to capture. Thus Stevens concluded that juvenile European Starlings are unable to gather enough animal food and therefore tried to compensate by eating the more accessible and energy-rich cherries. Similarly Breitwisch *et al.* (1987) have suggested that juvenile Northern Mockingbirds (*Mimus polyglottos*) may consume a considerable amount of fruit, because of the ease with which it may be obtained. It would be valuable to know if such a pattern exists in other opportunistically frugivorous species and if a disproportionate amount of frugivory results from inept juvenile foragers.

Walton (1979) suggested that a lack of juvenile capture skills might

explain age-related diet differences in Meadow Pipits (*Anthus pratensis*) during June when juveniles consumed more Coleoptera and Hymenoptera than did adults, but far fewer Dipetera (14% versus 47% for adults). The proportion of Coleoptera taken by juveniles in June and July (36% and 38%) was considerably higher than that taken by adults (19% and 22%). Walton noted that it is unlikely that juveniles were able to capture the more abundant but faster moving Diptera, while Coleoptera provided a scarcer, but more easily caught food supply. In an another case, juvenile Ospreys shifted their selection among size classes of fish over time (Edwards, 1989b). Initially, the juveniles selected the smallest size classes and ignored the largest. However, over time the juvenile Ospreys began to take more large fish. Edwards suggested that the initial absence of large fish in the diet was due to the inability of juveniles to capture large fish.

Another factor influencing juvenile diet selection is their limited handling abilities (see also Section 3.5). For example, because of their limited handling skills, small prey may be more profitable (energy gained/handling time) for juveniles whereas adult skills allow proficient handling of larger prey with profitabilities equivalent or larger than those of smaller prey (Sullivan, 1988b). Age-related differences in handling ability may explain many of the instances where juveniles feed on smaller prey items than those taken by adults. This tendency is widespread across a diversity of species, such as Great Blue Heron (*Ardea herodias;* Quinney and Smith, 1980), Gray Heron (Cook, 1978; Draulans, 1987), Cattle Egret (*Bubulcus ibis;* Siegfried, 1972), Ringed Plover (*Charadrius hiaticula;* Pienkowski, 1983), Eurasian Oystercatcher (Goss-Custard and Durell, 1983), Curlew Sandpiper (*Calidris ferruginea;* Puttick, 1978), Snail Kite (*Rostrhamus sociabilis;* Bourne, 1985), Osprey (Edward, 1989b), American Robin (Gochfeld and Burger, 1984), Northern Mockingbird (Breitwisch *et al.*, 1987), Northwestern Crow (Richardson and Verbeek, 1987), Yellow-eyed Junco (*Junco phaeonotus;* Sullivan, 1988b), Common Chaffinch (*Fringilla coelebs;* Kear, 1962), European Greenfinch (*Carduelis chloris;* Kear, 1962; Newton, 1967), and Eurasian Linnet (*Carduelis cannabina;* Newton, 1967). This widespread and possibly general phenomenon deserves more attention.

Age-related differences in diet could arise as a result of short-term persistence of diet specialization (Bryan and Larkin, 1972). This is suggested in the work of Edwards (1989b) who examined the ontogeny of diet selection in color-banded Ospreys. In the first year of the study, all young differed from adults with respect to diet selection, but in the second year 9 of 14 young differed from adults. Individual differences

in the diet selection of juveniles were present both years, with preference for each fish species in each year shown by at least one juvenile. Also, in both years some young exhibited no preferences for any fish species, but rather captured fish in relation to their availability. Interestingly, the diet preferences of individual juveniles remained constant throughout the postfledgling period while at the same time adults readily changed their diet in relation to fish abundance. The individual preference patterns of juveniles were related to whichever fish species were captured first. This suggests that the first few prey captured play an important role in initiating the development of a preference. Edwards suggests that this might lead to an early search image which could benefit juveniles by decreasing time and energy expended sampling for other prey. How long an individual juvenile's diet preference remains is unknown, but it would seem unlikely to persist for long once the birds arrive on their wintering grounds. Similar persistence in diet resulting from the earliest independent foraging experiences of juveniles has been documented in other species (Rabinowitch, 1968, 1969).

If diet selection involves the integration of information from all the foraging stages, then a lack of juvenile proficiency at any stage could have important consequences for the choice of diets by juveniles. It is likely that optimal diet selection in juveniles develops as rapidly as proficiency in other foraging activities (Richardson and Verbeek, 1987).

3.4. Prey Capture

The development of prey capture techniques, commonly proceeds from simple pecking to more complex capture movements often requiring considerable coordination and skill. For example, young Reed Warblers (*Acrocephalus scirpaceus*) initially captured insects with a stand and catch technique which declined in use with age, while leap catching and flycatching appeared later in development (Davies and Green, 1976). Northern Wheatears (*Oenanthe oenanthe*) initially used ground gleaning and stand gleaning motions to capture insects and only after the fifth day following fledging did they attempt the more complex perch-to-ground-sallying and aerial hawking movements, which are the common adult techniques (Moreno, 1984). Similarly, newly independent juvenile Northern Mockingbirds foraged primarily on the ground while adults used more aerial attacks to capture their insect prey; however juveniles increased their use of aerial techniques as the summer proceeded (Breitwisch *et al.*, 1987). Thus the capture techniques dependent upon flight performance are usually the last to develop. How-

ever, sometimes juveniles are capable of proficient prey capture by flight but use more energy conservative capture techniques than those used by adults (Davies and Green, 1976). For example, adult Reed Warblers may use more energy-demanding techniques (i.e., flycatching) in order to obtain sufficient food for their young as well as themselves.

Much of the initial improvement in capture success by young birds may be attributed largely to maturation (Cruze, 1935). However, once juveniles begin to feed independently, it is uncertain how important maturation is to the development of their capture proficiency. One case in which maturation has been correlated with improved capture skills in independent juveniles occurs in European Starlings (Stevens, 1985). The gradual improvements of juvenile capture skill is correlated with bill growth. This of course, does not eliminate the importance of learning from practice, which is likely to contribute to capture proficiency, sometimes long after most maturational changes have ceased (e.g., Richardson and Verbeek, 1987). Most workers have cited learning and practice as a cause, if not the major cause, of improved juvenile capture skill.

Generally, the greater the skill needed to capture prey, the less successful are juveniles in comparison with adults, and presumably a longer period of development is required. For instance, young Laughing Gulls were as successful as adults when snatching offal in the air, less successful when aerial dipping, and much less successful when plunge-diving for fish (Burger and Gochfeld, 1983). Not surprisingly, young Laughing Gulls most frequently used the method requiring the least skill and which provided them with highest success rate (aerial snatching of offal). In contrast, adult gulls most frequently used plunge-diving techniques for fish, presumably the method requiring the most skill. Similarly, young gulls of 15 different species avoided the most difficult foraging tasks such as plunge diving (Burger, 1987). When Sandwich Terns (*Sterna sandvicensis*) plunge dove from low heights into shallow water, no difference was found between adult juvenile capture success; however, when diving from greater heights into deeper water, with fish further below the surface, adult capture success was higher than that of juveniles (Dunn, 1972). In European Starlings, the difference in pecking success is large for difficult capture methods, such as grubbing, whereas little difference was found between age classes when catching prey on cow dung, a technique requiring relatively little skill (Stevens, 1985).

A commonly studied capture technique in which experience has been attributed to improved capture success is the plunge-diving method of Brown Pelicans, terns, gulls, and Ospreys (e.g., Orians, 1969;

Dunn, 1972; Buckley and Buckley, 1974; Burger and Gochfeld, 1983; Edwards, 1989a,b). Using this method a forager must contend not only with the evasive tactics of the prey, but with surface glare, refraction, and wind. Carl (1987) studied this technique in four age classes (yearlings; juveniles, 12–21 months; subadults 22–39 months; and adults) of Brown Pelicans, and found that both diving success and technique varied with age class. He showed that diving success among older birds improved with greater dive heights and steeper dive angles. He attributed the positive association between age and diving skills to several factors involving light physics, weather, neurological control, and learning. He noted that yearling pelicans may lack experience with changing marine conditions and perhaps lack the neurological coordination for high dives or steep angles. This lack of yearling diving proficiency restricts their choice of prey to those located near the surface and restricts the time of foraging. In contrast, older pelicans are able to exploit both shallow and deeper prey under a variety of conditions.

Experience with a capture technique may not always be the major factor responsible for improved juvenile capture success. For example, Coblentz (1986) describes a "midflight pause" in adult Brown Pelicans, which he suggests might allow a brief evaluation of the forager's probability of success with resumption of flight if success appears unlikely. Juvenile pelicans never showed a midflight pause prior to plunge-diving. This difference may have allowed adult pelicans to better discriminate against plunge-dives in which capture was unlikely, and thus contribute to the higher success of adults. Similarly, Buckley and Buckley (1974) concluded that the ability of adult Royal Terns to recognize capturable prey was a major factor in their fishing success. In this species both adults and juveniles had similar diving success (i.e., number of captures/dive), but adults increased their catch per unit time by increasing their diving rate to 1.6 that of juveniles. These two studies indicate that care must be exercised in interpreting capture success data because two different factors could be involved. Age-related capture differences may arise because of differences in ability to recognize capturable prey before a capture attempt, or because of actual differences in capture ability.

Under certain conditions, young foragers may be able to compensate for their lack of capture skills by obtaining food from other individuals. Begging is the obvious strategy for inept altricial young during the early period of parental care, but as they mature self-feeding becomes a more effective strategy, particularly as the parents become more reluctant to feed the young (Davies, 1976). Young Northern Wheatears switched between begging and self-feeding strategies on a

daily basis as they approached independence (Moreno, 1984). Early in the morning, when prey were inactive, the young wheatears chased their parents intensively for food, but switched to self-feeding around 0800 when rising temperatures led to an increase in insect activity and capture rates. However after 1000, capture success decreased, presumably due to faster moving insects evading capture, and the young returned to chasing their parents. Here Moreno demonstrated a clear relationship between the chasing and begging intensity of the young wheatears and their self-feeding success rates. These observations indicate that the young of altricial species may be able to choose the most profitable strategy according to their own ability to capture prey, at least during the end of the parental care period.

Another way in which juveniles might compensate for their lack of capture skills is by piracy or kleptoparasitism. Optimal foraging theory predicts that a forager will rob food only if the net energy gain from robbing exceeds or matches the net energy gained from feeding by other methods (Charnov, 1976; Dunbrack, 1979; but see Kushlan, 1978). Juveniles will at times resort to robbing, often more frequently than adults, as demonstrated in several studies. Verbeek (1977a,b) found that juvenile Herring Gulls feeding on refuse and on starfish were less skillful than adults and used chasing and stealing as an important method for obtaining food. Similarly, Greig *et al.* (1983) found that juvenile Herring Gulls made more attempts than adults to obtain food from other gulls, by displacement attacks and by intrusions onto the feeding patches of others, rather than searching the refuse itself. Juveniles were considerably less skillful than adults both in finding and obtaining food from refuse, whereas adults obtained almost all their food by searching the refuse pile itself. In another example, juvenile common Black-headed Gulls were less successful at robbing food from Northern Lapwings than were adults, and presumably as a result of their reduced success rate they attacked more often (Hesp and Barnard, 1989). However, when other feeding opportunities (e.g., feeding in plowed fields) arose, juveniles stopped robbing and adopted other foraging methods while adults continued to rob lapwings. In a similar manner, juvenile Bald Eagles (*Haliaeetus leucocephalus*) made more attempts at piracy from other eagles than did adults, possibly because juveniles are less proficient than adults at obtaining food independently (Fischer, 1985). Thus in these instances, juveniles probably rob to compensate for their inability to obtain other foods.

Other studies on several species of gulls have found that adults, rather than juveniles, were the most frequent pirates on conspecifics or other host species (Burger and Gochfeld, 1979, 1981). In their study of

piracy by four gull species, Burger and Gochfeld (1981) found that adults were victims less often than juveniles, and once chased, juveniles were more likely to lose their food than adults. This suggests that under the circumstances of their studies piracy by juveniles might be very costly, probably more so than for adults. Not surprisingly, juveniles appeared to be foraging in a different manner than adults—going after smaller food pieces (easier for them to handle), avoiding dense feeding flocks (where they are most likely to be attacked), and attempting piracy from other young. Such feeding behaviors may have provided the juveniles with alternative food sources as opposed to the relatively more costly piracy behavior.

Observations on piracy by juveniles are consistent with optimal foraging predictions suggesting that juveniles may compensate for their relatively inept foraging abilities by robbing, when the rewards from robbing are greater than other food sources, or switch to other food sources when the costs of robbing are too high. Unfortunately none of the current literature on age-related differences in piracy provides a test of the theory, which requires measurements of the net energy gained from robbing versus other food sources. To rigorously test the theory, studies using time and energy budget analysis are needed to determine the relative costs and benefits of prey robbing versus other feeding methods for juveniles and adults. Examples of the necessary approach are found in the studies of adult egret robbing behavior by Kushlan (1978) and Dunbrack (1979).

To be a successful pirate requires a variety of skills: the ability to identify potential victims, judging when to pursue a victim, the ability to follow the victim closely in flight, agility in flight, the ability to snatch food from the victim or to catch food dropped by the escaping victim, and knowing when to give-up an unsuccessful pursuit (Burger and Gochfeld, 1981). Most of these skills are likely to require experience and hence it is nor surprising that juveniles are frequently less proficient at robbing than adults (Burger and Gochfeld, 1979, 1981; Gochfeld and Burger, 1981; Hesp and Barnard, 1989), but not always (Verbeek, 1977a, b; Greig *et al.*, 1983). As mentioned previously, juveniles are sometime less proficient at identifying the most vulnerable victims (Carroll and Cramer, 1985). Judging when to pursue a victim appeared to be a difficulty for juvenile Common Black-headed Gulls when attacking Northern Lapwings for earthworms (Hesp and Barnard, 1989). In this case, juvenile gulls were less successful because their attacks were more likely to be mistimed and detected by the victim. Juveniles were also less selective in initiating long distance attacks and choosing vantage points within flocks. The method of approach largely

explains the difference in success between adult and juvenile Ring-billed Gulls (*Larus delawarensis*) pirating food from European Starlings (Burger and Gochfeld, 1979). Juvenile Ring-billed Gulls frequently walked toward Starlings, giving them time to fly off with food, whereas adult gulls were more likely to fly and hence startle the victim into dropping food. Adult Magnificent Frigatebirds (*Fregata magnificens*) were more likely to enter foraging gull flocks than were juveniles and consequently adults were more successful robbers (Gochfeld and Burger, 1981). In some gull species, adults were more likely to abandon unsuccessful piracy attempts earlier in the act than were juveniles (Verbeek, 1977b; Burger and Gochfeld, 1981). It thus appears that experience, at all stages of the robbing process, is crucial for obtaining proficiency.

Social interactions between adults and juveniles may reduce juvenile capture success. For instance, once juveniles have obtained food by robbing or capture they are often more likely to be victims and lose more food when pursued by adults (Burger and Gochfeld, 1981; Gochfeld and Burger, 1981; Carroll and Cramer, 1985; but see Schnell *et al.*, 1983). Under certain circumstances, it may be advantageous for juveniles to forage together in flocks in the absence of adult interference, as suggested for Royal Terns, White Ibis (*Eudocimus albus*), and Crimson Rosellas (Buckley and Buckley, 1974; Bildstein, 1983; Magrath and Lill, 1985). For example, juvenile Common Black-headed Gulls feeding in flocks without adults foraged more efficiently than juveniles in flocks with adults (Ulfstrand, 1979). Even when in mixed-age flocks, juvenile White Ibis were more likely to have juveniles as nearest neighbors than adults, although this did not appear to influence their foraging proficiency (Bildstein, 1983). Sometimes within mixed-age flocks, juveniles tend to hunt on the flock periphery, presumably as a result of adult dominance (e.g., Bildstein, 1983; Gochfeld and Burger, 1984). If this is so, it suggests that a peripheral location is disadvantageous, possibly because of lower food densities or because higher levels of vigilance are required (Bildstein, 1984). Thus the tendency for juveniles to be subordinate to adults may also contribute to their lower capture proficiency.

Foraging in a group often confers a variety of benefits, including improved foraging success (for a review see Morse, 1980). However, juveniles often lack the skills necessary to take advantage of the benefits of group foraging. For example, in Great Blue Herons, adult foraging success was greater in flocks of more than five individuals, while juvenile success was not related to flock size (Quinney and Smith, 1980). In Black-necked Stilts (*Himantopus mexicanus*), individuals feeding in

groups obtained more food than those feeding nearby, and those that fed near dense flocks obtained more food items than juveniles that fed solitarily (Burger, 1980). Burger suggests that perhaps the group movement stirred up insects, making food generally more available to members of the flock. Juvenile stilts frequently fed solitarily, while adults rarely fed outside the groups, suggesting that adults learn that group foraging is more efficient. However, in other circumstances juveniles can benefit by foraging in a group. The benefits of group foraging by juveniles are apparent in Yellow-eyed Juncos in which Sullivan (1988a) showed that independent juveniles foraging alone scanned more than juncos in flocks, and consequently had lower pecking rates than those foraging in flocks. She concluded that the juvenile's increased pecking rates when foraging in flocks may be attributable, in part, to their decreased scanning rate, but local enhancement, social facilitation, and copying are probably also involved. In Ospreys, capture success improves more rapidly among siblings that forage together than in siblings that forage solitarily (Edwards, 1989a). Furthermore, sibling Ospreys had similar capture techniques suggesting that socially facilitated learning was involved. These studies indicate that under some circumstances juvenile foraging proficiency may be aided by group foraging, while under other circumstances juvenile foraging proficiency does not appear to improve while foraging in a group.

In summary, prey capture proficiency improves with maturation, experience, and coordination. Complex capture techniques are likely to require considerable time for development, mostly because the predator requires time to obtain experience. Inept juvenile foragers may seek alternative capture methods or diets to compensate for their lack of capture skills. Certain social interactions with other foragers have the potential to accelerate the development of juvenile capture proficiency, but adult piracy and dominance may inhibit juvenile proficiency.

3.5. Food Handling Time and Techniques

Handling time is the time required for a forager to eat a captured food item, and is a widely used measure of time and energy investment by foragers (Krebs *et al.*, 1983). Handling time can represent a substantial portion of the foraging time for many species such as raptors, gulls, parrots, oystercatchers, shrikes, titmice, finches, and corvids. Among adults, handling time is known to vary with size of prey, bill size, hunger, competition, previous experience, the need for vigilance, and the risk associated with dropping items (Krebs, 1980; Barnard and Stephens, 1981; Sherry and McDade 1982; Paszkowski and Moremond,

1984; Greig-Smith, 1984). Considering the variety of factors which can influence food handling times it should not be surprising that adults and juveniles often differ in their food handling abilities.

Juveniles of a variety of species and diet types (piscivores, insectivores, mollusc eaters, scavengers, carnivores, seed eaters) have been found to be less adept at handling food items than adults. For instance, juveniles have a tendency to drop food items more frequently than adults (Buckley and Buckley, 1974; Barash *et al.*, 1975; Davies and Green, 1976; Burger, 1981; Greig-Smith, 1985; MacLean, 1986), and juveniles frequently have longer handling times than adults (Davies and Green, 1976; Ingolfsson and Estrella, 1978; Gochfeld and Burger, 1981; Bourne, 1985; Sutherland *et al.*, 1986; Richardson and Verbeek, 1987; Enoksson, 1988; but see Greig-Smith, 1985). In some species, adults and juveniles have equivalent handling times with small prey items, but adults are noticeably faster than juveniles when handling larger prey items (Quinney and Smith, 1980; Sullivan, 1988b). Furthermore, the development of food-handling proficiency can be a slow process and consequently is often one of the last feeding skills to develop in certain birds (e.g., rosellas, Cannon, 1979; three gull species, MacLean, 1986).

Improvement in juvenile handling time and ability can largely be attributed to learning and to maturation. For example, Davies and Green (1976) demonstrated that naive hand-reared Reed Warblers were less adept at handling flies (longer times and more dropping) than were experienced warblers; yet naive and experienced warblers were equally capable of catching flies. Although the naive warblers did improve their handling skills with time, they never obtained the proficiency of the experienced birds. Davies and Green suggested that a sensitive period in the early stages of growth, when the bill was flexible, allowed rapid development of handling skills in contrast to later life when the bill was less flexible. The combination of bill maturation (i.e., growth in length) and experience were also cited as the reason for improved handling skills of juvenile European Nuthatches (*Sitta europaea*) in the field (Enoksson, 1988).

An instance of the importance of food handling experience during a sensitive period has been documented in shrikes. For example, in young Loggerhead Shrikes learning how to impale or wedge prey is by imprinting (S. M. Smith, 1972). These birds use a type of behavior designated as dabbing in which they take an item of food, turn sideways and place it on their perch. Dabbing begins at about 21 days after hatching and after approximately 36 hours of this behavior the young shrikes add pulling components—young turn sideways, reachout, then

pull the food item along the perch toward them (dragging behavior). Initially there is no orientation to this behavior, but when the food item accidently catches on something, the young shrike concentrates its dragging efforts along that part of the branch in which the food item was snagged. Thus the young shrikes quickly learn to direct their dragging to appropriate places such as forks or thorns. However, this learning must occur within a critical period; those young shrikes having experience between 20 and 40 days posthatching all learned to impale normally, but those raised in cages with dowel perches until 75 days posthatching did not learn how to impale,, even when provided with the opportunity to observe experienced shrikes impale food items nearby. Also, young shrikes seem to prefer the kind of impaling device with which they were raised, even when it is less efficient (Wemmer, 1969).

The relative importance of self-learning in the development of prey impaling and wedging varies among different species of shrikes as shown in a comparative study of European shrikes (Lorenz and von St. Paul, 1968). For example, personal experience appeared to be unimportant to Red-backed (*Lanius collurio*) and Woodchat Shrikes (*L. senator*) before being able to direct dragging behavior to thorns (impaling), but both required experience before learning to direct dragging to branch forks (wedging). The opposite pattern was found in Northern Shrikes (L. excubitor) in which inexperienced young directed dragging to forks, but they required experience to impale items on thorns. Lorenz and von St. Paul argued that these patterns were consistent with the natural history of the three species.

Possibly one of the most complex forms of food handling behavior is the shell-dropping behavior of gulls, rooks, crows, and Lammergeyers (*Gypaetus barbatus*) used to break open hard-shelled prey to consume the edible inner parts. The complexity of this behavior results from the need for many different decisions if the forager is to obtain the maximum rate of net energy intake for its efforts. Each of the following must be selected by the forager: the size and type of food item for dropping, a suitable substrate on which to drop the item, an appropriate height from which to drop the item, and the number of times to drop an item before giving up if it does not break (Barash *et al.*, 1975; Siegfried, 1977; Zach, 1979; Kent, 1981; Maron, 1982; Richardson and Verbeek, 1987). Therefore, considering the complexity of this behavior it should not be surprising that it takes considerable time for young birds to obtain the proficiency of adults.

Juveniles appear to be less skilled than adults at almost all stages of the shell-dropping process. For example, first year Herring Gulls and Glaucous-winged Gulls differed from adults (> 2 years) by dropping

more food items on inappropriate substrates (soft sand or water) and by dropping items from a greater range of heights which is disadvantageous because items dropped at great heights are more likely to be stolen and those dropped from low heights are unlikely to break (Barash *et al.*, 1975; Ingolfsson and Estrella, 1978). Furthermore, yearling Glaucous-winged Gulls were more likely than adults to "accidently" drop clams while flying. Yearling Northwestern Crows took more time to drop clams than adults and required more drops to break them open (Richardson and Verbeek, 1987).

Learning in various forms appears to play a prominent role in the improvement of juvenile shell-dropping behavior. Initially, observational learning and imitation from the parents might be important as the young birds follow their parents after fledging (Richardson and Verbeek, 1987). Yearling gulls sometimes attempt to rob prey from older birds engaged in shell-cracking (Verbeek, 1977b), which might aid in associating the shell-breaking pattern with hard surfaces (Ingolfsson and Estrella, 1978). However, after the period of parental association, trial-and-error learning is likely to account for most of the refinement of a youngster's shell-dropping skills. Consistent with the likelihood of a trial-and-error learning process are the accounts of yearling birds dropping shells only to retrieve them again in midair, dropping items without investigating the results, dropping items while standing on the ground, dropping two items at once, and making flights similar to drop flights, but without actually releasing an object (Ingolfsson and Estrella, 1978; Richardson and Verbeek, 1987). In contrast to the importance of learning, maturation appears to be an unlikely explanation for the lack of juvenile proficiency in shell-dropping behavior—juveniles at fledging have a mass similar to adults and their flight capabilities appear to be similar within a few months of fledging (Barash *et al.*, 1975; Richardson and Verbeek, 1987).

Another suggested factor contributing to the lack of juvenile proficiency in shell-dropping behavior is related to potential problems arising from overspecialization as a juvenile (Olive, 1982). Richardson and Verbeek (1987) have elaborated on this idea by suggesting that a lack of juvenile proficiency might arise from the need to retain behavioral plasticity until reaching maturity. They state that proficiency at a skill like shell-dropping obtained during an early age might be maladaptive if it inhibits the development of proficiency in some other specialized skill later in life. Unfortunately, they provide no examples to support this idea, and thus it presently appears to be untested.

It appears that most *simple* food handling skills, such as using the feet to hold food items by titmice (Vince, 1960) and opening seed by

finches (Kear, 1962; Newton, 1967), can develop independently of interaction with other individuals, including the parents. However, as the food handling process becomes more complex it seems likely that learning from parents or other individuals is important, as suggested previously for shell-dropping behavior. The classic example of the importance of learning a food-handling skill from the parents is that of the Eurasian Oystercatcher in which the young develop the same mussel feeding techniques of their parents (Norton-Griffiths, 1967, 1969). Young oystercatchers whose parents stab mussels develop the stabbing technique while those whose parents hammer develop the hammering technique. Norton-Griffiths showed that the young learn the method of opening mussels from their parents by switching the eggs of hammers and stabbers. Although oystercatchers acquire the favored mussel opening technique of their parents, they will at times use other techniques (Goss-Custard and Sutherland, 1984). How the young actually learn the necessary skills is unknown, but young using either of the two mussel feeding techniques remain with their parents 18–26 weeks whereas those oystercatcher young feeding on other prey stay with their parents for only 6–7 weeks. It thus appears that this specialized handling technique has the cost of requiring a longer period of parental care. Another instance where parental interaction might prove important is in the rapid development of food handling skills in fish-eating birds such as the Common Tern (*Sterna hirundo*) studied by Gochfeld (1980). He suggested that the consistency with which parents present fish to newly hatched young might enhance the development of the chick's ability to handle and manipulate food items. This untested idea would appear amenable to experimental testing.

That the limited food handling abilities of juveniles can influence their diet choice was nicely demonstrated by Sullivan (1988b) in a detailed field study of age-specific food handling times and prey profitability in Yellow-eyed Juncos. Sullivan presented four different age classes of juncos (recently independent juveniles, young experienced juveniles, old experienced juveniles, and adults) with large and small mealworms and measured handling times. She found that handling times were significantly related to both mealworm size and age class. The large mealworms took significantly longer to handle than the small mealworms for all age classes of juncos. Recently independent juveniles took longer to handle the large mealworms than either age class of experienced juveniles. Adult juncos took significantly less time to handle the large mealworms than did experienced juveniles. She next used the handling times to calculate the profitability (joules/second) when foraging on small and large mealworms within each junco age class.

Her profitability calculations indicated that for recently independent juveniles, small mealworms were much more profitable than large mealworms and, not surprisingly, these birds selected significantly more small mealworms than large mealworms. However, for the other three age classes, small and large mealworms were equally profitable and these birds displayed no preferences in mealworm size. Thus the diet of adults and juveniles may differ because of differences in the relative profitability of prey for each age class, arising primarily from differences in prey handling ability.

Sullivan's (1988b) profitability analysis is likely to be important for understanding why juveniles tend to select similar prey items than adults in a wide variety of species (see Section 3.3). For example, Great Blue Herons fit the pattern of juvenile selection of smaller prey than adults, and furthermore juveniles and adults have equivalent handling times for small prey, but adults are quicker with larger prey (Quinney and Smith, 1980). In this case too, it is likely that the smaller prey are more profitable for juveniles because of their inept handling of larger prey, which are preferred by the adults. It would be valuable to determine the profitability of different sizes and types of prey items for adults and juveniles of those species in which juveniles tend to prefer smaller prey items or prey types than adults.

Handling skills may influence habitat or patch selection if prey sizes and types are not evenly distributed between localities. This occurs in adult oystercatchers in which the two prey handling types ("hammers" and "stabbers") feed in the mussel beds appropriate to their respective handling skills (Norton-Griffiths, 1967). Handling differences might account for habitat or patch differences between adults and juveniles, particularly if inept handling skills restrict juveniles to a particular prey type, and if that prey type is limited to certain patches or habitats. This hypothesis has not yet been fully confirmed in the field. Bourne's (1985) field study of Snail Kites would seem to have many of the necessary requisites: juveniles have longer handling times, juveniles select smaller snails, and juveniles select different habitats than adults. However, Bourne concluded that there was no support for the hypothesis that kite diet differences are caused by handling time differences, although he provided no alternative explanation.

Finally, the lack of food-handling proficiency of young birds can have major implications for survival. The lack of food-handling skills can increase the likelihood that food items will be stolen, as a result of longer handling times (Gochfeld and Burger, 1981; Barnard and Thompson, 1985) or due to inept handling (Barash *et al.* 1975), thereby resulting in more time and energy expended in foraging. Moreover,

inept and careless food-handling will require greater time and energy expenditure for foraging by juveniles, thus exposing them to greater risks of predation or making it difficult to acquire sufficient energy (Sullivan, 1989). Thus if food-handling behavior is one of the last foraging skills to develop it could serve as a major constraint on proficiency for a variety of species requiring complex food-handling abilities.

4. DISCUSSION

So far we have seen that juveniles may be less proficient than adults in selecting a foraging site, in search behavior, in food recognition and diet selection, in capture methods, and/or in handling techniques. However, few studies have examined the relative contribution of these components to age-related foraging differences. One notable exception is the work of Sutherland *et al.* (1986) which compares the relative importance of encounter rate with handling time in contributing to adult/juvenile differences in foraging rates by Common Moorhens (*Gallinula chloropus*). Juvenile moorhens take longer to pick up and swallow items and are less efficient at finding food while searching. To examine the relative importance of these two foraging components, Sutherland *et al.* used Holling's (1959) equation for the number of prey found (N_a) in time (T) at a given encounter rate (λ) and handling time (H_t):

$$N_a = \frac{\lambda \bullet T}{1 + \lambda \bullet H_t}$$

By altering handling time or encounter rate, this expression can be used to assess the relative contribution of handling time and encounter rate to adult/juvenile foraging differences. For instance, juvenile moorhens found 31.7 items in 120 s. If juveniles had the same handling times as adults they would locate 35.6 prey in 120 s, producing an improvement of 11%. If they had instead the same encounter rate as adults they would find 49.7 per 120 s, for an improvement of 36%. Therefore in this case the age difference in encounter rate was more important than the difference in handling time in accounting for the difference in feeding rate.

The real contribution of the Sutherland *et al.* (1986) analysis, however, is in reemphasizing the importance of food density to the relative contribution of the two foraging components to adult/juvenile foraging differences. They note that the encounter rate is a combination of food density and a forager's ability to find it. Hence, doubling the food densi-

ty will double the encounter rate. At very high food densities, and consequently high encounter rates, the feeding rate will be limited by handling time. In other words, at high food densities, the feeding rate will be the reciprocal of handling time and the discrepancy in encounter rate will be irrelevant. In contrast, at very low food densities the handling time will be trivial and the encounter rate will be the important determinant of feeding rate.

Consistent with these predictions are the results of Draulans (1987) which demonstrated that yearling Grey Herons were less successful (measured as success and frequency of strikes) than adults at low prey densities, but that yearlings obtained a foraging performance similar to adults at high prey densities in fish farm ponds. Draulan found no age-related difference in handling times and attributed the juveniles' relative lack of success at low prey densities to their lower encounter rates which included prey recognition and capture skills. Thus at high prey densities, age differences in foraging may be trivial in those species in which adults and juveniles do not differ in handling times. More importantly, this finding emphasizes that not all age-related proficiency differences are important, at least under certain conditions.

Most of the field studies of age-specific foraging differences have been conducted in the post-breeding period (fall or winter in the temperature zone) when prey densities are likely to be relatively low. At this time, age-related foraging differences are likely to be evident for species in which younger individuals are relatively inept at encountering prey, due to a lack of proficiency in selection of foraging site, search pattern, prey recognition, and/or capture. However, few studies (but see Orians, 1969) of age-related foraging differences have been conducted during the breeding season when food densities might be expected to be highest, and consequently inept prey-encounter abilities are less of a hindrance to the proficiency of younger foragers. Therefore it is conceivable for some species (those with no or minor age differences in handling), that age-related differences become trivial during the breeding season when high prey densities make the inept encounter abilities of yearlings, second-year, and third-year birds irrelevant. Studies are needed to test this possibility particularly because the inept foraging ability of younger individuals is commonly cited as a reason for delayed breeding in many birds (reviewed in Ryder, 1980; Burger, 1988).

To understand the mechanisms involved in the development of foraging proficiency it is valuable to examine the sequence in which the various aspects of foraging behavior are improved (e.g., Davies and

Green, 1976). MacLean (1986) has described this sequence in three gull species (all unbanded) and found that the rate at which juveniles obtained proficiency in the different foraging stages varied between species. He found in Bonaparte's Gull (*Larus philadelphia*) that search and pursuit improved simultaneously and handling skills improved later. In the Ring-billed Gull, searching ability improved first, followed by pursuit and capture abilities, and handling improved last. In contrast, pursuit improved first in Herring Gulls followed by handling and searching abilities. What accounts for these species differences was left unexplained, but future studies are likely to uncover more species differences in the sequence in which the different aspects of foraging behavior are improved. Studies of additional species may allow us to use the comparative method to identify the factors controlling the sequence in which foraging proficiency is obtained.

As demonstrated throughout this chapter, lack of experience is the factor most likely to hinder juvenile foraging proficiency, and its effect is greatest for the methods requiring the most skill for mastery. For piscivores, raptors, and kleptoparasites the greatest skills are probably required for recognizing capturable prey, the actual capture technique, and sometimes handling. Foragers picking prey items from a surface or probing below the surface must be most adept at prey recognition, although handling skills may become paramount if the food is encased in a protective covering. In contrast, searching skills are likely to be most important for nectarivores. Therefore, the foraging stage or stages requiring proficiency is dependent upon the prey type. As a forager's diet becomes more variable, it is likely to require higher levels of skill at more stages of the foraging sequence. This of course, requires experience, which takes time and hence is costly to develop. Thus the necessity of mastering many different skills requiring experience limits how broad or general an individual forager's diet may become.

A stable food supply will encourage individual specialization on particular foraging skills, which can enhance foraging proficiency (Partridge and Green, 1985, 1987). For example, recent experiments with Jackdaws (*Corvus monedula*) demonstrated that specialization improves foraging efficiency (Partridge and Green, 1987). In this study, hand-reared birds were trained to be either "specialist" feeders on one of three artificial laboratory feeding tasks or "generalist" feeders on all three. The results indicated that the specialist birds were usually more efficient at obtaining food from their tasks than were the generalists. This suggests that specialization enhances foraging proficiency and, in addition, diet specialization may improve digestive efficiency (Par-

tridge and Green, 1985). These advantages may encourage short-term diet specialization, even in juveniles (e.g., Edwards, 1989b), or lead to individual diet specialization (Partridge and Green, 1985).

If the idea that specialization enhances foraging proficiency is a general phenomenon, then it suggests that specialist juveniles may obtain adult levels of proficiency at faster rates than generalist juveniles. A rigorous test of this hypothesis is not presently possible because of the limited number of studies with marked birds, necessary for an accurate determination of juvenile development rates. However, some of the present studies are consistent with the hypothesis. For instance, the highly specialized handling skills used by Eurasian Oystercatchers to open muscles may be obtained by juveniles in only a few months (Goss-Custard and Durell, 1987a; *contra* Norton-Griffiths, 1969). In contrast, most gull species have a generalized diet and in some species juveniles do not obtain adult levels of proficiency until after three years (MacLean, 1986; Burger, 1987). A valuable test of the hypothesis, might be made by comparing the rate at which young gulls (i.e., extreme generalists) obtain adult levels of proficiency while plunge-diving with the rate at which proficiency is obtained by specialist plunge-divers (Brown Pelicans, Ospreys, terns).

As a consequence of their inept foraging abilities, juveniles are likely to spend more time foraging than adults (Schreiber, 1968; Spaans, 1971; Davis, 1975; Verbeek, 1977b; Cook, 1978; Morrison *et al.*, 1978; Puttick, 1979; Burger and Gochfeld, 1979; Burger, 1980; Ryan and Dinsmore, 1980; Porter and Sealy, 1982; Schnell *et al.*, 1983; Magrath and Lill, 1985; MacLean, 1986; Sutherland *et al.*, 1986; East, 1988; Sullivan, 1988a). Accordingly, adults often spend more time resting than juveniles, presumably as a result of their better foraging skills (Buckley and Buckley, 1974; Schnell *et al.*, 1983; Magrath and Lill, 1985; MacLean, 1986; Sutherland *et al.*, 1986; Sullivan, 1988a). However, sometimes juveniles loaf more, possibly watching for adult feeding flocks (Porter and Sealy, 1982). Such observations suggest that juveniles may have difficulty in maintaining a positive energy budget, which is consistent with the findings that starvation is a major cause of juvenile mortality in a variety of species (e.g., Lack, 1966; Southern 1970; Hirons *et al.*, 1979; Perrins, 1980; Sullivan, 1989; Catterall *et al.*, 1989). In addition, as juveniles forage more in an effort to maintain a positive energy budget they become more prone to predation. This may occur because juveniles will tolerate greater risks in obtaining food (e.g., Caraco *et al.*, 1982; Schneider, 1984), decrease their vigilance (e.g., Lendrem, 1983; East, 1988; Sullivan, 1988a), and accelerate their re-

turn to feeding areas after the passage of a predator (e.g., Hegner, 1985; de Laet, 1985; East, 1988). The time period during which juvenile foraging inefficiency accounts for much of their increased mortality is virtually unknown for most species (however, see Sullivan, 1989), but is valuable for understanding avian survivorship and population regulation.

5. SUMMARY

We know that juveniles can be less proficient than adults in their selection of foraging sites, search patterns, recognition and selection of food, and in capture and handling techniques. In all species which have been examined, age-related differences in foraging proficiency have been found in at least one aspect of foraging behavior. We frequently do not know the relative importance of these differences. Unfortunately, for only a very few species do we know the rate at which foraging proficiency improves, the factors influencing this rate, and whether predictable species differences occur in foraging development rates. Experience, necessary for both cognitive and motor skills, is the factor most likely to delay the juvenile's acquisition of adult levels of foraging proficiency. Sometimes, juveniles compensate for their inept foraging skills and differ from adults by foraging in different sites, selecting different sizes and types of food, using different capture methods, resorting to piracy, and/or joining feeding groups. While these age-related foraging differences have been reasonably well documented, we generally do not know the conditions in terms of cost of benefits which encourage or prevent these juvenile foraging differences. Because juveniles are usually subordinate to adults they are sometimes displaced from the prime foraging sites, prevented from taking the most profitable prey, and/or more likely to be victims of piracy. Therefore adult dominance may interact with the juvenile's inept foraging skills, and contribute to the inability to obtain an optimal diet or maintain a positive energy budget. Untangling the effects of adult dominance and the juvenile's lack of foraging skills is a difficult task for field workers concerned with identifying the factors contributing to high juvenile mortality rates and has been accomplished in only a few studies with marked individuals. Finally, experimentation and laboratory studies have yet to fully contribute to solving problems associated with the acquisition of foraging proficiency by juvenile birds.

1. APPENDIX: Summary of Species in Which Age-Related Differences in Foraging Proficiency Have Been Documented*

Brown Pelican (*Pelacanus occidentalis*)

Orians (1969). Plunge-diving. PR, PS, PC. Adults had higher capture success in dry season (60% vs. 49%) but not in wet season (57% vs. 61%).

Schnell *et al.* (1982). Plunge-diving. PR, PS, PC. Adults had higher success (84% vs. 75%).

Brandt (1984). Plunge-diving. FS, PR, PS, PC. No difference in foraging site use, adults had higher capture success (83% vs. 49%).

Carl (1987). PR, PS, PC. Adults had higher capture success (14% vs. 8%).

Olivaceous Cormorant (*Phalacrocorax olivaceus*)

Morrison *et al.* (1978). Surface diving, FS, PR, PS, PC. Adults had higher success rates in two habitats (18% vs. 10% and 19% vs. 12%).

Magnificent Frigatebird (*Fregata magnificens*)

Gochfeld and Burger (1981). Piracy of gulls, PR, PS, PC, PH. Adults had higher capture success (13% vs. 4%). Adults had shorter handling time (1.9 vs. 6.0 s).

Great Blue Heron (*Ardea herodias*)

Quinney and Smith (1980). Striking fish, PR, PS, PC. Adults took larger prey and had higher capture success (62–77% vs. 14–33%).

DesGranges (1981). Striking fish, PR, PS, PC. Adults had higher capture success (80% vs. 52%).

Grey Heron (*Ardea cinerea*)

Cook (1978). Striking fish, FS, PS, PC. Adults foraged in different sites and had higher capture success (50% vs. 29%).

Draulans and Van Vessem (1985). Striking fish, FS. Adults foraged in different sites than juveniles.

Draulans (1987). Striking fish, PS, PC, PH. Adults took larger prey and capture success differences were related to prey density; no age differences in prey handling.

Little Blue Heron (*Egretta caerulea*)

Recher and Recher (1969). Striking fish, FS, PR, PS, PC. No differences in foraging site but juveniles had more misses per strike and hence less g/min intake.

Cattle Egret (*Bubulcus ibis*)

Siegfried (1972). Insect gleaning, PR, PS, PC. In this diet study, adults took larger prey and had more food in their guts than juveniles.

Green-backed Heron (*Butorides striatus*)

Higuchi (1986). Bait fishing. Juveniles used inappropriate bait.

White Ibis (*Eudocimus albus*)

Bildstein (1983). Probing for crabs, FS, PR, PS, PC. Age differences in foraging site were found and yearlings had a capture rate 40% of the adult rate.

Bildstein (1984). Probing for crabs, PR, PS, PC. Second year birds had a capture rate 60% of the adult rate.

Osprey (*Pandion haliatus*)

Edwards (1989a). Plunge-diving, PR, PS, PC. Sibs had greater capture success than singletons, but singletons eventually caught up; sibs had similar capture techniques.

Edwards (1989b). Plunge-diving, FS, PR, PS. Juveniles differed from adults in foraging sites and diet; juveniles selected their diet on the basis of their first capture.

Snail Kite (*Rostrhamus sociabilis*)

Bourne (1985). Snail capture, FS, PH. Juveniles differed from adults in foraging site, took smaller snails, and had longer handling times regardless of snail size.

Northern Harrier (*Circus cyaneus*)

Bildstein (1987). Aerial attack and pounce on terrestrial prey, S, PC. No age difference in foraging site or capture technique. Juveniles differed from adults in temporal pattern of foraging, foraging height and speeds, and had lower capture success.

Sharp-shinned Hawk (*Accipiter striatus*)

Mueller and Berger (1970). Aerial attack, PR, PS. Juveniles took inappropriate prey.

European Sparrowhawk (*Accipiter nisus*)

Barnard (1979). Aerial attack, PC. A juvenile used innappropriate technique and made more prey passes than an adult.

Common Moorhen (*Gallinula chloropus*)

Sutherland *et al.* (1986). Surface picking, PR, PS, PC, PH. Adults had a higher capture rate (89 items/min vs. 40 items/min) and shorter handling times than juveniles.

American Coot (*Fulica americana*)

Ryan and Dinsmore (1980). Surface picking. Time budget analysis indicates that yearlings and second year birds spend more time feeding than third year birds.

Northern Lapwing (*Vanellus vanellus*)

Barnard and Thompson (1985). Surface picking, PR, PS, PC. Juveniles differed from adults in having lower capture rates and longer handling times. Juveniles were more likely to be victims of gull attacks.

Masked Lapwing (*Vanellus miles*)

Burger and Gochfeld (1985b). Surface picking, S, PR, PS, PC, PH. Interfood time interval was less for adults and juveniles pecked more without success.

Ringed Plover (*Charadrius hiaticula*)

Pienkowski (1983). Surface picking, S, PS, PC, PH. Juveniles differed from adults by having shorter waiting and giving-up times, took smaller, less variable prey, and lower pecking rates. Handling ability improved with age.

Eurasian (Northern Pied) Oystercatcher (*Haematopus ostralegus*)

Norton Griffiths (1967, 1968, 1969). Mussel probing, FS, PS, PH. Juveniles required 3 years to acquire adults levels of handling proficiency; juveniles learn mussel opening method of parent, either stabbing or hammering, which influences foraging site selection.

Goss-Custard *et al.* (1982), Goss-Custard and Durell (1983, 1987a, b, c). Mussel and other invertebrate probing, FS, PS, PH. Age difference found in foraging site use, diet selection, and handling ability. Juveniles were displaced by adults on prime mussel beds, so juveniles took different prey in different patches and were more likely to lose food to older birds.

Black-necked Stilt (*Himantopus mexicanus*)

Burger (1980). Surface/subsurface pecking, PR, PS, PC, PH. Interfood intervals were shorter for adults than juveniles, but only at mid-day; juveniles spent more time and energy foraging than adults at certain times of day.

Black-winged Stilt (*Himantopus himantopus*)

Espin *et al.* (1983). Surface/subsurface pecking, PS, PR, PC, PH. Adults have a higher capture succes rate and move more slowly than juveniles, but do not differ in handling times.

American Avocet (*Recurvirostra americana*)

Burger and Gochfeld (1986). Pecking and Scything, FS, PR, PS, PC. Juveniles were most similar in capture times to adults in habitats where adults were most efficient. Capture time (time to obtain 10 prey items) was shorter for adults under all conditions.

Ruddy Turnstone (*Arenaria interpres*)

Groves (1978). Surface pecking, FS, PR, PS, PC. Adults had higher foraging rates and success in two sites than juveniles in both sites; adults had higher foraging rates (.22/s vs. .19/s and .38/s vs. .25/s) and success rates (.19/s vs. .16/s and .26/s vs. .16/s) than juveniles. Adults were dominant to juveniles.

Curlew Sandpiper (*Calidris ferruginea*)

Puttick (1978). Substrate probing, PR, PS. Stomach analysis indicates that juveniles took smaller prey items than adults.

Puttick (1979). Substrate probing, FS, PR, PS, PC. No difference in foraging site; adults had higher foraging rate (43 vs. 28 probes/min) and higher success rate (10 vs. 4 prey items/min) than juveniles.

Gulls—15 species

Burger (1987). Variety of foraging methods, PR, PS, PC, PH. Interfood interval used for comparison. Adult interfood interval was shorter in all but 5 feeding situations. Variance in interval was explained by age, species, food type, method, and habitat.

Laughing Gull (*Larus atricilla*)

Burger (1981). Dump foraging, PR, PS, PC, PH. No age differences in success rate due to attacks by other gulls. Juveniles were more likely to drop food items.

Burger and Gochfeld (1981). Piracy, PR, PS, PC, PH. Adults had higher success as

pirates; adults less likely to be victims; adults more likely to pirate large items and keep them; juveniles more likely to steal from other juveniles; juveniles more likely to drop items and took longer to handle food than adults.
Burger and Gochfeld (1983), Burger (1987). Different foraging methods (aerial snatching, aerial dipping, plunge-diving), FS, PR, PS, PC, PH. Adults differed in success in relation to habitat; juveniles concentrated in habitats where their interfood interval was closest to adults. Adults had shorter interfood intervals and higher success rates than did juveniles.
Carroll and Cramer (1985). Piracy from pelicans, PR, PS. Adult gulls preferred juvenile pelicans as victims; juvenile gulls selected their victims at random.
Burger and Gochfeld (1985). Dump foraging, S, PR, PS, PC, PH. Adult interfood interval is shorter than juveniles when not overwhelmed by pirates. When overwhelmed by pirates no differences occurred.

Common Black-headed Gull (*Larus ridibundus*)

Ulfstrand (1979). Surface picking for worms, S, PR, PS, PC, PH. Adult success rate (items/min) was higher than juvenile rate; juvenile success rate was higher in pure juvenile flocks than in mixed adult/juvenile flocks due to adult interference.
Burger (1987). Different foraging methods. Interfood time interval was shorter for adults except when aerial dipping for invertebrates on a bay.
Hesp and Barnard (1989). Piracy on lapwings, FS, PS, PC. Adults often in lapwing flocks while juvenile sometimes foraged in plowed fields; juveniles tended to select their victims at the wrong time; juveniles mistimed their attack and thus had lower success rates than adults (21.7–22.3% vs. 39.4–53.1%).
Amat and Aguilera (1990). Piracy on egrets, stilts, and godwits, PS. Juveniles more likely to attack stilts while adults preferentially attack godwits. Adults force juveniles to use suboptimal victims (stilts).

Bonaparte's Gull (*Larus philadelphia*)

MacLean (1986). Plunge-diving, S, PR, PS, PC, PH. Juveniles had higher search times, lower capture efficiency, longer interfood intervals, and were more likely to drop items than adults. He documented juvenile improvements over time.
Burger (1987). Different foraging methods. Interfood interval was shorter for adults than juveniles, except when picking up insects from a mudflat.

Ring-billed Gull (*Larus delawarensis*)

Burger and Gochfeld (1979, 1981). Piracy on starlings, PS, PC. Adults were more successful than juveniles or subadults (66% success vs. 33% vs. 36%). Adult success was due to use of an effective method (flight), while juveniles were more likely to walk.
MacLean (1986). Plunge-diving, S, PS, PC, PH. Juvenile search time was longer; adults were more successful at prey capture, had shorter interfood interval, but juveniles improved with time; juveniles were more likely to drop items. He showed that juveniles improved with time.
Burger (1987). Different foraging methods. Interfood interval shorter for adults in all foraging situations.
Burger and Gochfeld (1985). Dump foraging. Interfood interval shorter for adults under all conditions.

California Gull (*Larus californicus*)

Porter and Sealy (1982), Plunge-diving and dipping, PR, PS, PC. Adult success rate was higher than rate for subadult or juvenile (95% vs. 76% vs. 26%). Juveniles used local enhancement to find food.

Burger (1987). Different foraging methods. Adult interfood interval was shorter than interval for juveniles under all conditions.

Herring Gull (*Larus argentatus*)

Verbeek (1977a). Dump digging, S. Adults moved more items when searching for food and thus encountered more food items/min than juveniles.

Verbeek (1977b). Plunge-diving for starfish, PS, PC. Adults had higher capture efficiency than juveniles (64% vs. 16%).

Ingolfsson and Estrella (1978). Shell-dropping, PH. Juveniles were less likely to crack shells on the first drop (43% vs. 65%) and less likely to be successful after several attempts.

Burger (1981). Dump foraging, PR, PS, PC, PH. Foraging efficiency (items/attempt) varied with age (adults, 58% vs. subadults, 28% vs. juveniles 35%). Juveniles were more likely to drop items and were more likely to attempt piracy than adults.

Burger and Gochfeld (1981). Piracy on gulls. Adults were pirates more often than juveniles; adults were successful pirates more often; adults were victims less often; once chased juvenile were more likely to drop food.

Greig *et al.* (1983). Dump foraging, S, PR, PS, Adults turned over objects more quickly than juveniles; juveniles walked more per food item (133 paces/item vs. 41 paces/item) than adults. Juveniles were more likely to use displacement attacks for food.

Burger and Gochfeld (1985). Dump foraging, S PR, PS, PC, PH. Adult interfood interval was shorter than interval for juveniles, but only when not overwhelmed by pirates. If overwhelmed by pirates no age differences were found.

MacLean (1986). Plunge-diving PR, PS, PC, PH. Juveniles showed more intention movements; interfood interval shorter for adults; capture efficiency was lower for juvenile, but improved with time; juveniles were more likely to drop food items.

Burger (1987). Different foraging methods. Adults had shorter interfood intervals except when picking worms from a surface.

Glaucous-winged Gull (*Larus glaucescens*)

Barash *et al.* (1975). Clam dropping, PH. Juveniles were more likely to drop clams in flight (29%) than adults (7%) and they were more likely to to drop items on the wrong substrate and from the wrong height.

Searcy (1978). Plunge-diving, PR, PS, PC. Adults were more efficient than subadults or juveniles (69% vs. 50% vs. 44%).

Burger (1987). Different foraging methods. Adult interfood interval was shorter than the interval for juveniles under all conditions.

Royal Tern (*Sterna maxima*)

Buckley and Buckley (1974). Plunge-diving, S, PR, PS, PC, Ph. Adults covered the feeding area more quickly, were more likely to recognize capturable prey, and thus caught more prey per unit time than did juveniles. Juveniles were more likely to drop prey items. Capture success rate did not differ with age.

Sanwich Tern (*Sterna sandvicensis*)

Dunn (1972). Plunge diving, PR, PS, PC, PH. Adults had a higher capture success than juveniles (17% vs. 13%) and higher capture rate (.24 captures/min vs. .16 captures/min). There was no difference in the rate of diving and juveniles were more likely to drop prey.

Crimson Rosella (*Platycercus elegans*)

Magrath and Lill (1985). Insect and plant gleaning. FS, PS. Juveniles fed in different sites and took more insects than adults which fed on fern sori. Time budget analysis indicated that juveniles spent more time feeding.

Northwestern Crow (*Corvus caurinus*)

Richardson and Verbeek (1987). Clam dropping, S, PS, PH. Juveniles spent more time searching than adults (64 s vs. 35 s), took smaller clams, required more drops to break clams (2 drops vs. 1.7 drops/clam), and thus obtained ⅓ the net energy intake of adults.

Rook (*Corvus frugilegus*)

East (1988). Seed-eating, FS, PR, PS, PC, PH. Juveniles foraged in different sites and were initially slower at consuming grain (65 vs. 133 s) than adults, but eventually obtained the same consumption rate.

European (Wood) Nuthatch (*Sitta europaea*)

Enoksson (1988). Seed-eating, PH. In summer juveniles took fewer seeds per visit than adults (1.4 vs. 2.2), but no difference in October.

Reed Warbler (*Acrocephalus scirpaceus*)

Davies and Green (1976). Insect gleaning and flycatching, PR, PS, PC, PH. Juveniles initially pecked at all objects, but quickly became selective; capture success improved with age; naive birds were more likely to drop prey, but handling time and ability improved with age.

Spotted Flycatcher (*Muscicapa striata*)

Davies (1976). Insect gleaning and flycatching, PR, PS, PC. Juvenile capture success improved with time and hence they relied less on begging from parents.

Northern Wheatear (*Oenanthe oenanthe*)

Moreno (1984). Insect gleaning and flycatching, PR, PS, PC. Naive juveniles initially pecked at inedible objects, and their capture success improved with age.

Eastern Bluebird (*Sialia sialis*)

Goldman (1975). Perch-to-ground sallying and flycatching, PR, PS, PC. Adults had higher capture success than juveniles (67% vs. 32%).

American Robin (*Turdus migratorius*)

Gochfeld and Burger (1984). Soil probing for invertebrates, S, PR, PS, PC. Juveniles took more steps per bout than adults, took smaller prey items, and juvenile capture success was 75% that of adults. Juveniles took 136% as long to capture each item, and required 161% as many steps as adults, obtained 25% less food per unit time.

Northern Mockingbird (*Mimus polyglottos*)

Breitwisch *et al.* (1987). Ground gleaning and perch-to-ground sallying, PR, PS, PC. Adults took larger prey and had higher capture success (70% vs. 25%) than juveniles. Adults used more aerial attacks, but juveniles increased aerial attacks over time.

European Starling (*Sturnus vulgaris*)

Stevens (1985). Ground probing and pecking, S, PR, PC. Juveniles more likely to feed on fruit, possibly due to ease of capture. Adults had higher capture success when feeding on invertebrates (177 mg prey/100 pecks vs. 35 mg).

Silvereye (*Zosterops lateralis*)

Jansen (1990) Insect gleaning and probing, PR, PS, PC. Older birds had higher success rate than first-year birds for all capture techniques and substrates except dead leaves and bark. Second-year birds had higher success rate than first-year for gleans and in needles.

Bananaquit (*Coereba flaveola*)

Wunderle and Soto (1987). Nectar feeding, S, PR. Juveniles were more likely to re-visit a previously visited flower than were adults.

Wunderle and Lodge (1988). S, PR. Juveniles made more flower revisitations than expected by chance alone; adults made fewer flower revisitations than expected by chance. Movement patterns of adults were different than those of juveniles.

Yellow-eyed Junco (*Junco phaeonotus*)

Sullivan (1988a). Picking insects from the ground, PS, PR, PC, PH. Juveniles initially had higher pecks per capture than adults, but reached adult levels by independence. Time budget indicated that juveniles spent more time searching for, pecking at, and handling food items than adults.

Sullivan (1988b). Picking insects from the ground, PS, PH. Juveniles selected smaller mealworms than adults, and took less time to handle small prey than large. In contrast, adults took less time than juveniles to handle large prey items. Age-related diet differences were due to the relative profitability of each prey for each age class.

Weathers and Sullivan (1989). Picking insects from the ground. Time and energy analysis indicates that adults obtain nearly three times as much energy per hour foraging as recently independent juveniles (14.5 vs. 5.3 kJ/h).

Red-winged Blackbird (*Agelaius phoeniceus*)

Beauchamp *et al.* (1987). Search in three choice maze, S. Adults were more likely to return to the site where they were initially rewarded with food and in which food supply was not depleted. Juveniles returned at random.

Eurasian Bullfinch (*Pyrrhula pyrrhula*)

Greig-Smith (1985). Fruit and seed eating, FS, PS, PH. No age differences in foraging site, but adults ate more ash seeds and juveniles more likely to drop food items.

*Given for each reference is foraging mode and any differences for the following foraging components: foraging site (FS), search (S), prey rec-

ognition (PR), prey selection (PS), prey capture (PC), and prey handling (PH).

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