

DEVELOPMENT OF FORAGING SKILLS AND THE TRANSITION TO INDEPENDENCE IN JUVENILE SAVANNAH SPARROWS

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Abstract. We investigated the timing and pattern of the development of foraging skills in juvenile Savannah Sparrows (*Passerculus sandwichensis*). Juveniles of known age, parentage, and in some cases sex were mist netted and tested in an aviary on Kent Island, an isolated island in the Bay of Fundy, Canada. Captive birds were exposed to three standardized and ecologically relevant foraging tasks: locating spittle bugs (Homoptera: Cercopidae) in spittle masses on goldenrod (*Solidago rugosa*) plants, small caterpillars under spruce (*Picea glauca*) bud scales, and beetle larvae under leaves. The feeding trials involved 33 juveniles aged 17–42 days, four independent juveniles whose precise ages were not known, and five adults for comparison. The performance of juvenile sparrows on all three tasks showed rapid improvement between 22 and 24 days of age. Thereafter, foraging proficiency (number of foraging attempts, number of prey obtained, foraging efficiency) did not improve significantly with age among juveniles; in fact, older juveniles performed as well as adults. Juvenile males obtained more prey items than juvenile females in aviary trials. Foraging proficiency in captivity was not a good predictor of survival to the following year, and it appeared not to be influenced by brood membership or parental age. The age at which foraging performance improved in captivity coincided with the age at which parents cease attending their fledglings in the field, suggesting that the duration of postfledging parental care may be determined by the speed at which juveniles can develop foraging skills.

Key words: foraging, independence, juvenile birds, *Passerculus sandwichensis*, postfledging, Savannah Sparrows.

Desarrollo de Destreza para Forrajear y Transición a la Independencia en Juveniles de *Passerculus sandwichensis*

Resumen. Investigamos el tiempo y el patrón de desarrollo de destreza para forrajear en juveniles de *Passerculus sandwichensis*. Se capturaron y se evaluaron juveniles de edad, origen, y (en algunos casos) sexo conocidos en una pajarera en Kent Island, Bahía de Fundy, Canadá. Las aves capturadas se expusieron a tres tareas de forrajeo estandarizadas y ecológicamente relevantes: localizar insectos (Homoptera: Cercopidae) en su espuma en hierbas (*Solidago*), orugas pequeñas en las ramitas de *Picea glauca*, y larvas de escarabajo debajo de hojas. Utilizamos 33 juveniles de 17–42 días de edad, 4 juveniles independientes de edades desconocidas y 5 adultos para comparar. El desempeño de los juveniles en las tres tareas mostró una mejoría rápida entre 22 y 24 días de edad. A partir de entonces, la competencia al forrajear (número de intentos de forrajeo, número de presas obtenidas, eficiencia de forrajeo) no mejoró significativamente con la edad entre los juveniles; de hecho, los juveniles mayores se desempeñaron tan bien como los adultos. Los machos juveniles consiguieron más presas que las hembras en las pruebas. La competencia al forrajear en cautiverio predijo la sobrevivencia hasta el siguiente año adecuadamente, y pareció no ser influenciada por la nidada a que se pertenecía o por la edad de los padres. La edad en que la competencia al forrajear mejoró en cautiverio coincidió estrechamente con la edad en que los padres dejan de cuidar a los volantones en el campo, lo cual sugiere que la duración del cuidado de los padres después de que los polluelos salen del nido puede ser determinada por la rapidez con que los juveniles puedan desarrollar destreza para forrajear.

INTRODUCTION

In most measures of foraging performance, recently fledged birds tend to be less adept than adults, presumably because proficient foraging

requires experience and well-developed muscular, skeletal, and neurological systems (Marchetti and Price 1989). The speed at which juveniles acquire foraging skills has important implications for the evolution of avian life histories. To the degree that juveniles must rely on their parents until they can forage on their own, postfledging parental care may have to be extended,

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broods may have to be divided between parents, overall costs of reproduction may rise, and reproductive rates may be reduced (Weathers and Sullivan 1991, Langen 2000). Postfledging parental care may last for weeks or even months (e.g., White-winged Cough [*Corcorax melanorhamphos*]; Heinsohn 1991, Gill 1995). For species capable of producing two broods per year, prolonged postfledging parental care of the first brood may delay initiating a second clutch until conditions are less favorable, or it may foreclose the option of producing a second clutch altogether (Verhulst and Hut 1996). If parents have to divide their brood in order to feed their young until the young can forage for themselves (Edwards 1985, Byle 1990), natural selection may favor biparental care and enforce monogamy (Freeman-Gallant 1996).

Although age-specific differences in foraging behavior have been documented in various species (Barraud 1961, Davies and Green 1976, Greenberg 1987, Clayton 1994), there are few quantitative studies of how and when foraging skills develop in birds in the wild (Weathers and Sullivan 1989, 1991, Jansen 1990, Yoerg 1994, 1998). Nice's (1943) observations of hand-raised Song Sparrows (*Melospiza melodia*), which were among the earliest descriptive accounts of the ontogeny of foraging in songbirds, are probably representative of many passerines. They paint a picture of a growing interest in self-feeding and exploration beginning at about 12–13 days, although foraging is tentative and ineffective at that stage. About a week later, Song Sparrows improve rapidly in motor and foraging abilities. Difficult skills such as cracking seeds develop more slowly than abilities such as handling insect prey (Nice 1943, Marchetti and Price 1989).

The purpose of our study was to document the development of foraging skills in Savannah Sparrows (*Passerculus sandwichensis*) under natural conditions. We present data on age-specific foraging behavior in wild juvenile sparrows which we captured and tested in an aviary. We also explore whether foraging proficiency develops differently between juvenile males and females, whether it depends upon the type of foraging situation, whether it predicts survival to the following year, and whether there is any evidence of the inheritance of foraging abilities or the influence of a common brood environment. Finally, we examine the hypothesis that

the amount of time fledglings require to develop foraging skills corresponds to (and possibly dictates) the duration of postfledging parental care in nature.

METHODS

STUDY SITE AND SPECIES

Savannah Sparrows occur at high densities on Kent Island, New Brunswick, Canada, an 80-ha island located 9 km south of Grand Manan Island (44°35'N, 66°46'W). Our study site is two fields, 1.5 and 6 ha in size, in the center of the island (see Wheelwright and Mauck 1998 for detailed descriptions of field methods and the study site). Females build cryptic nests on the ground in open habitats. If their first clutch is successful, females typically lay a second clutch 1–3 weeks after fledging young from the first. The young leave the nest 9–12 days after hatching (median = 10 days), at which point the parents generally divide the brood, each caring for 1–3 fledglings (Wheelwright and Rising 1993, Wheelwright et al. 2003). Fledglings initially remain within their natal territory, where they are fed and accompanied by their parents. After becoming independent about two weeks later (23.4 ± 4.3 days of age, $n = 96$; Wheelwright et al. 2003), juveniles join loose flocks composed almost exclusively of hatch-year Savannah Sparrows, which wander around the island until they depart on their southward migration 4–8 weeks later (Wheelwright et al. 1994). The breeding biology of Savannah Sparrows on Kent Island is generally similar to that of mainland populations except for higher population densities, greater natal philopatry, lower nest predation rates, and more foraging in spruce (*Picea glauca*) trees surrounding open habitats on the island (Wheelwright and Rising 1993, NTW, unpubl. data).

The Kent Island Savannah Sparrow population lends itself to studies of the postfledging period. Juveniles are abundant and confined to the isolated island, so it is not difficult to follow and recapture marked individuals for several weeks after fledging. Natal philopatry is high: ca. 11% of 7-day-old nestlings and 25% of independent juveniles return to breed on the island the following year, so it is possible to relate behaviors such as foraging proficiency to survival (Wheelwright and Mauck 1998).

Beginning in 1987, we have captured all nestlings and adults in the study site during the

breeding season, measured them, and marked them with U.S. Fish and Wildlife Service aluminum bands and plastic color bands (Wheelwright and Mauck 1998). Therefore, we knew the ages and identities of all parent birds and most of the juveniles in this study (some juveniles raised elsewhere on Kent Island disperse into the study area once they become independent; the precise ages of these birds are not known).

By 10 days of age (i.e., at fledging), tarsus length in Savannah Sparrows equals that of adult birds and remains relatively constant thereafter. However, other aspects of body size (including traits directly related to foraging, such as bill length and depth) are distinctly smaller, even at independence two weeks after leaving the nest (NTW, unpubl. data).

SUBJECTS AND APPARATUS

Between 14 and 30 July 1997, we mistnetted 37 juvenile Savannah Sparrows to test their ability to perform foraging tasks in captivity. Thirty-three of the juveniles had been banded as nestlings; their ages ranged from 17 to 42 days (mean \pm SD: 30.1 ± 7.1). The other four juveniles, whose ages we estimated (on the basis of tail length; NTW, unpubl. data) to be 35–40 days, were independent of their parents and had wandered into the study area. We also netted and tested five adults for comparison. Birds were captured in the early morning and held in separate cages ($30 \times 30 \times 30$ cm) in a shed until testing took place later the same day. Prior to testing, birds were provided with five mealworms (*Tenebrio* sp.) per hour, plus *ad libitum* water and millet seeds. Seven of the juveniles (all younger than 24 days old) did not attempt to feed during the experiments and were therefore excluded from certain analyses (e.g., foraging efficiency). A maximum of four birds were held at any one time. After testing, subjects were released where they had been captured or, in the case of juveniles younger than 20 days old, in the vicinity of their parents. Younger juveniles were usually separated from their parents for no more than 1–2 hr; older juveniles were generally released within 2–4 hr. During this project, we adhered to guidelines of the Animal Behavior Society and Association for the Study of Animal Behavior for the ethical treatment of animals, the legal requirements of Canada, and the guidelines of Bowdoin College.

The sex of Savannah Sparrows can be determined with 94% accuracy by the time they reach 26 days of age, using measurements of wing length and body mass and a discriminant function (Wheelwright et al. 1994, Wheelwright and Seabury 2003). For juveniles that returned the following year as adults, we confirmed sex by the presence of a brood patch or cloacal protuberance. Our sample of known-age juveniles included 16 females and 10 males; the other seven birds were too young to sex with confidence and did not return the following year. There were two male and two female juveniles of unknown age. All five adults tested were males. The sample of juveniles included four pairs of siblings, three groups of three siblings, and two groups of four siblings. Four of these 25 juveniles were too young to forage in the experiments, so we were left with 21 juveniles from eight broods to examine the effect of a common nest or post-fledging environment on foraging abilities. Siblings were rarely tested on the same day, so our analyses were not confounded by similarity in age of siblings. Because for a few birds we knew neither the age nor sex, or were unable to record foraging attempts, sample sizes vary between analyses.

We tested the birds in a small aviary ($150 \times 75 \times 75$ cm) attached to the side of the holding shed. An observer sat inside the shed and viewed the birds through a one-way mirror (45×45 cm). Half of the aviary floor was covered with grasses and ferns; the floor of the testing side was bare wood. The exterior walls and roof of the aviary were constructed of hardware cloth partially covered with vegetation to provide cover for the birds. Experiments were conducted under ordinary weather conditions.

Each bird was presented with three foraging tasks which involved finding hidden insect prey. The tasks corresponded to foraging maneuvers normally practiced by juvenile and adult Savannah Sparrows during the breeding season (Wheelwright and Rising 1993): capturing (1) spittlebugs (Homoptera: Cercopidae) in a mass of spittle on the stems of rough goldenrod (*Solidago rugosa*) ("goldenrod task"); (2) spruce budmoth larvae (Lepidoptera: Olethreutidae, *Zeiraphera* sp.) under the bud scales covering the terminal needles of white spruce twigs ("spruce task"); and (3) invertebrate prey under leaves on the ground ("leaf task"). For the goldenrod task, each bird had to peck into a mass of

spittle located ca. 5 cm above the cut base of a goldenrod stem in order to capture a late-instar (ca. 6 mm long) spittlebug nymph. Five fresh stems, collected in the field with naturally occurring spittle masses, were held upright in holes drilled 6 cm apart in a block of wood (30 × 8 × 3 cm). Birds could stand on the block to probe the spittle mass but could not cling to the stem itself or see the insects. For the spruce task, birds had to remove the bud scales capping the terminal needles of a 6–8 cm spruce twig to obtain the prey. Half of a mealworm (4–6 mm) was substituted for spruce budmoth larvae because by late July not all twig tips contained larvae. We constructed artificial bud scales out of masking tape painted brown because real bud scales were too fragile to remove and replace for subsequent trials; preliminary experiments showed that artificial and natural scales were handled in the same fashion. Five fresh spruce twigs were held horizontally in the same wooden block described above, turned on its side so that the twigs were approximately 4 cm above the floor of the aviary. Birds could stand on the floor to peck at the bud scales but could not perch on the stem. For the leaf task, birds had to remove half of a mealworm concealed in a shallow well (2-cm diameter, 0.5-cm deep) beneath a goldenrod leaf (ca. 2 × 6 cm). One fresh leaf covered each of five wells drilled 5 cm apart in a block of wood (35 × 9 × 1.3 cm). The goldenrod and spruce tasks, which required probing specific targets, could be considered more directed tasks compared to the leaf task, which could be solved by probing under the leaf, tearing it, or lifting it by scratching. Each task provided five prey items.

PROCEDURE

Each bird was placed in the aviary to acclimate 30 min prior to the start of the foraging trials. Millet seeds and water were available *ad libitum* during this acclimation time. In addition, five mealworm halves were placed on the floor of the aviary in order to determine whether the birds could be tested on a foraging task. If the mealworms were not eaten within 30 min, the seeds were removed and the bird was given an additional 30 min to eat the mealworms. If the bird did not touch the mealworms during that time, it was assigned performance scores of 0 for all three tasks and returned to its parents (none of these birds was older than 19 days; preliminary

experiments showed that birds that did not pick up mealworms during the first hour of testing would not succeed at any of the foraging tasks). Food, water, and foraging tasks were added and removed through a small window at one side of the aviary. Most birds reacted little to the disturbance, other than moving to the far side of the aviary; all birds resumed normal behavior within 1–2 min.

Each bird was tested only once on each foraging task in order to reduce the effects of experience and learning. The order of task presentation was randomized over subjects to control for order effects. At the start of a trial, we placed one task type onto the test floor. The bird was given 10 min to begin foraging on the task. If the bird did not begin to forage within this time limit, the task was removed and the next task was introduced 5 min later. If the subject failed to forage during all trials (most of these birds, all younger than 24 days old, remained stationary instead, uttering begging calls), it was assigned task performance scores of 0 for all three tasks and released. However, if any one of the three tasks was attempted, the bird was given one more opportunity to attempt each missed task.

When the bird made its first foraging attempt (probing a spittle mass, bud scale, or leaf with its bill, or scratching at a leaf with its feet), it was given a maximum of 10 min more to forage. The trial ended as soon as the 10 min had expired or the bird had attempted all five prey locations, whether it obtained prey or not. At the end of each trial, the task was removed and there was a 5-min break before the start of the next trial. The observer was blind to the age, sex, and brood membership (i.e., relatedness to other subjects) of the birds being tested.

We used a handheld event recorder (Macintosh Newton 130, with the program Ethoscribe, Tima Scientific, Halifax, Nova Scotia) to determine the time of different behaviors and count the number of foraging attempts (including repeated attempts at the same location) and the number of prey items obtained at each task. The latter score was confirmed following the trial by examining each of the five feeding locations for prey. From these data we calculated foraging efficiency (number of prey obtained/number of foraging attempts) for each individual at each task.

STATISTICAL ANALYSES

We used repeated measures ANOVA to determine the effect of age class (juvenile versus adult) and task type (goldenrod, spruce, or leaf) on foraging performance, and ANOVA to determine the effect of brood membership on foraging performance (SAS Institute 1999). Spearman rank correlations were used to examine changes in foraging performance with juvenile age. Mann-Whitney *U*-tests were used to compare the foraging performance of males versus females, and juveniles that returned the following year versus birds that failed to return. Because of strong natal and breeding philopatry in the Kent Island population, birds that do not return are likely not to have survived (see Wheelwright and Mauck 1998). Data are presented as means \pm SD.

RESULTS

We tested 37 juveniles and five adults in feeding trials. All three birds younger than 20 days of age begged steadily but made no attempt to feed on the available mealworms prior to the trials. All other birds advanced to the testing sessions. Two birds aged 20 days and two aged 23 days did not touch the spittle mass, spruce bud scales, or goldenrod leaf and thus were also assigned performance scores of 0 for each trial. One 22-day-old bird foraged successfully during the aviary trials. Thus, none of five birds younger than 22 days, and only one of eight birds younger than 24 days, attempted to forage. In contrast, every bird older than 23 days attempted to forage from at least one of the tasks ($n = 30$ juveniles and 5 adults; Fig. 1). Therefore, in the analyses that follow, we examine separately the foraging behavior of all juveniles and the subset of "older juveniles" (birds 24–42 days old).

Foraging attempts consisted of pecking, probing, pulling, or tearing at the spittle mass, spruce bud scales, or goldenrod leaf, as well as the "double-scratch" technique, in which the bird hops once toward the task and then scratches backward with both feet (Gobeil 1968, Wheelwright and Rising 1993). The feet did not always come into contact with the task when this was performed. Double-scratching occurred mainly during the leaf task, as juveniles attempted to turn over goldenrod leaves. However, some older juveniles occasionally double-scratched during the spruce task as well, despite the fact that the spruce twigs were elevated beyond

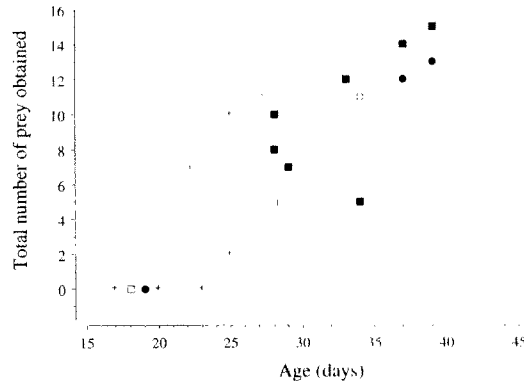


FIGURE 1. Total number of prey items obtained during three foraging tasks by juvenile Savannah Sparrows of different ages. There were five prey items per task for a maximum possible score of 15. Squares = individuals that did not return the following year; circles = returning individuals. Solid symbols = males; unfilled symbols = females. Crosses = nonreturning juveniles (not sexed). The crosses at 20 days and 23 days represent two individuals each. The number of prey obtained was positively correlated with age over all juveniles but independent of age among the subset of juveniles 24–42 days old.

reach of their feet. Once a bird discovered a prey item during one of the tasks, it tended to find other prey items rapidly.

The number of foraging attempts during all tasks combined increased with age among juveniles ($r_s = 0.47$, $n = 33$, $P < 0.01$). However, once juveniles reached the age at which they regularly fed during the foraging trials (older juveniles), the number of foraging attempts did not change significantly with age ($r_s = 0.09$, $n = 25$, $P = 0.65$). Comparing the foraging behavior of older juveniles with that of adults, the number of foraging attempts was independent of age class but not task type (repeated measures ANOVA: age: $F_{1,28} = 2.6$, $P = 0.11$; task: $F_{2,56} = 4.1$, $P = 0.02$; Fig. 2a). Both older juveniles and adults made more attempts to forage on the leaf task than on other tasks. Over all task types, there was no difference between older juveniles and adults in number of foraging attempts (Mann-Whitney $U = 31$, $n = 25$ older juveniles and 5 adults, $P = 0.08$).

As with foraging attempts, the number of prey items obtained among all juveniles during all tasks combined increased significantly with age ($r_s = 0.58$, $n = 33$, $P < 0.001$; Fig. 1). However, among older juveniles, there was no correlation

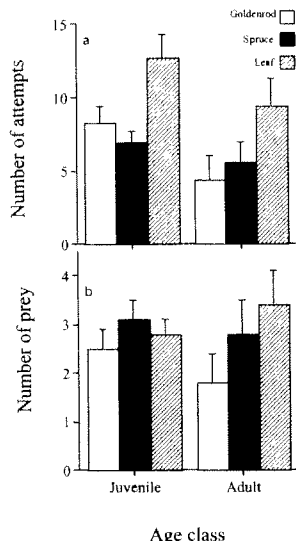


FIGURE 2. (a) Mean \pm SE number of foraging attempts during three foraging tasks by older juvenile (24–42 days old; $n = 30$) and adult Savannah Sparrows ($n = 5$). (b) Mean number of prey items obtained by older juvenile and adult Savannah Sparrows. Once juveniles had reached the age of 24 days, they performed as well as adults in the foraging trials.

between the number of prey obtained and age ($r_s = 0.19$, $n = 25$, $P = 0.34$). The effect of task type on the number of prey items obtained was not significant (repeated measures ANOVA: age class: $F_{1,28} = 0.07$, $P = 0.80$; task: $F_{2,56} = 2.0$, $P = 0.15$; Fig. 2b). Combining the number of prey obtained across all task types, there was no difference between older juveniles and adults (Mann-Whitney $U = 58.5$, $n = 25$ older juveniles and 5 adults, $P = 0.82$).

Foraging efficiency (number of prey obtained per foraging attempt) did not increase with age among older juveniles ($r_s = 0.10$, $n = 25$, $P = 0.62$). The effect of age class and task type on foraging efficiency was not significant (repeated measures ANOVA: age class: $F_{1,23} = 3.2$, $P = 0.09$; task: $F_{2,46} = 2.9$, $P = 0.07$). Over all task types, there was no difference between older juveniles and adults in foraging efficiency (Mann-Whitney $U = 47$, $n = 25$ older juveniles and 5 adults, $P = 0.39$).

With regard to differences between the sexes among older juveniles, males and females made a similar mean total number of foraging attempts and showed similar foraging efficiency (attempts: Mann-Whitney $U = 56.6$, $P = 0.68$; ef-

iciency: $U = 33.5$, $P = 0.06$; $n = 9$ males and 14 females). However, males obtained more total prey during the foraging trials than females (10.7 ± 3.4 versus 7.4 ± 3.4 ; Mann-Whitney $U = 31.5$, $P < 0.05$; Fig. 1), even though their ages did not differ (33.8 ± 4.5 days versus 33.5 ± 4.3 days; Mann-Whitney $U = 57.5$, $P = 0.73$). Although there was substantial variation between older juveniles in total number of attempts and prey items obtained, there was no detectable effect of brood membership on number of attempts, number of prey items, or foraging efficiency (ANOVA: attempts: $F_{7,13} = 0.7$, $P = 0.68$; prey: $F_{7,13} = 1.9$, $P = 0.15$; efficiency: $F_{7,12} = 0.79$, $P = 0.62$). Neither the total number of attempts nor the number of prey obtained by older juveniles was correlated with the ages of their mother or father, or with their parents' ages combined ($n = 33$, all $P > 0.28$). Older juveniles that returned the following year ($n = 5$) had performed no better in foraging trials than juveniles that failed to return ($n = 20$; Mann-Whitney $U = 39$, $P = 0.45$; Fig. 1).

DISCUSSION

Our experiments with juvenile Savannah Sparrows captured in the field indicate that it takes about 12–14 days after leaving the nest for young birds to acquire basic foraging skills. Although the limited sample size does not allow us to rule out the possibility that birds younger than 22 days of age lacked the motivation (rather than the skill) to forage proficiently under the solitary experimental conditions, numerous observations of clumsy or inappropriately directed foraging efforts by such young Savannah Sparrows in both the field and aviary suggest that differences in motivation due to the experimental conditions are an insufficient explanation (see also Nice 1943, Weathers and Sullivan 1989, 1991). Moreover, we observed rapid improvement of foraging ability, with captive juveniles making their first successful foraging attempts at 22–24 days of age. No birds younger than 22 days, and only one of eight birds younger than 24 days, even attempted to forage during the aviary trials, whereas all 30 birds older than 24 days attempted to forage. This pattern strongly suggests a developmental threshold in foraging proficiency. However, it would be necessary to increase the sample size between ages 20 and 25 to determine how abrupt the transition to independent foraging is. Similarly, given the varia-

tion between individual juveniles, it would be useful to reconfirm our finding that there was no correlation between age and any measure of foraging performance among juveniles after the age of 23 days. Juveniles older than 23 days appeared to be as capable of solving simple foraging tasks as adults.

In contrast to our results, most field studies describe foraging efficiency increasing incrementally over the postfledging period (Davies 1976, Moreno 1984, Weathers and Sullivan 1989). Similarly, laboratory studies in which parents and offspring are not separated show a gradual development in foraging proficiency (Wortis 1969, Hirose and Balsam 1995). Gradual increases in juvenile foraging proficiency may characterize bird species that must master particularly difficult specialized foraging skills (Langen 2000). It may be that, for Savannah Sparrows, learning to feed on seeds and insects is easy compared, for example, to capturing underwater prey by Eurasian Dippers (*Cinclus cinclus*), a species where foraging proficiency develops gradually (Yoerg 1994, 1998). Alternatively, differences between our results and previous studies may be due to the conditions under which we tested foraging abilities by juvenile Savannah Sparrows, particularly the confinement of experimental subjects to a relatively small space with food items placed in a conspicuous location and no conspecifics with which to interact.

Studies showing gradual development of foraging proficiency in the field may also partly be the result of parents slowly decreasing the amount of food provided as their offspring mature, in effect subsidizing them until they improve their foraging skills. In many bird species, offspring at first increase but later decrease the amount of begging directed toward their parents as the parents become reluctant to provide food to their fledglings and begging becomes less profitable than foraging independently. A rise in "parental meanness" has been shown to play an important role in the transition to offspring independence in hand-reared Great Tits (*Parus major*; Davies 1978). By making it more difficult for young tits to obtain food by begging, Davies (1978) experimentally decreased the age at which the rate of self-feeding increased. Likewise, in Northern Wheatears (*Oenanthe oenanthe*), as parents gradually reduce the rate at which they feed their offspring, the offspring spend

more time calling and chasing after their parents. As chasing becomes less successful, independent feeding increases (Moreno 1984; but see Burger 1980, Yoerg 1998). In any case, testing juveniles in captivity in isolation from their parents, as in our study, eliminated young juveniles' ability to gain food by begging and did not incorporate a gradual decline in parental feeding in our measure of juvenile acquisition of foraging skills.

The absence of an effect of brood membership or parental age on foraging proficiency in our study suggests that variation in simple foraging proficiency does not have a strong heritable component and that it is only weakly influenced by nest environment or the quality of postfledging parental care. Similarly, foraging proficiency (as indicated by our aviary experiments) was a poor predictor of survival to the following year. Of course, these results do not mean that more complicated foraging behaviors lack a genetic basis, that their learning is unaffected by parental experience, or that they do not influence the probability of survival.

The timing of the acquisition of foraging skills in our aviary experiments was closely related to the age at which Savannah Sparrows reach independence in the field. Under natural conditions, parents stop feeding their offspring at a median of 23 days posthatching (although postfledging parental care can continue until fledglings are 35 days old; Wheelwright et al. 2003). This also corresponds to the age at which fledglings first appear in all-juvenile flocks in the absence of their parents (Wheelwright and Rising 1993). Thus, the ability to forage independently apparently occurs just prior to the age at which parents cut off care. Although we found in the aviary experiments that juvenile males obtained more prey than females of the same age, in the field males and females acquire independence at the same age (Wheelwright et al. 2003). At independence, juvenile males have levels of testosterone that are higher than juvenile females (and similar to that of adult males during the incubation stages, O'Reilly and Wheelwright, unpubl. data). Sexual differences in foraging performance in captivity may be due to hormonal influences on motivation or other behaviors (e.g., quicker habituation to the experimental conditions, higher activity levels).

The fact that all juvenile Savannah Sparrows in this study could solve simple foraging tasks

by the time they were 24 days old raises the question of why some parents continue to care for their fledglings for as much as 10 additional days. Presumably survival in the field requires many more skills than the simple challenges presented in our experimental trials, skills that require time or teaching by parents to master. Alternatively, juveniles may feign dependence even when they are capable of foraging independently, as has been observed in Reed Warblers (*Acrocephalus scirpaceus*; Davies and Green 1976) and Northern Wheatears (Moreno 1984). It is not unusual in the field to see juvenile Savannah Sparrows as old as 35 days begging from adults. Parents that extend postfledging care beyond the acquisition of basic foraging skills may provide a critical supplement to offspring during harsh weather or severe food shortages (perhaps especially on islands, Higuichi and Momose 1981).

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