



Skill acquisition and the timing of natal dispersal in the white-throated magpie-jay, *Calocitta formosa*

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*(Received 1 January 1995; initial acceptance 16 March 1995;
final acceptance 7 July 1995; MS. number: A7224R)*

Abstract. Offspring may remain associated with parents to gain the skills required for independent survival and reproduction. The ontogeny of foraging and breeding behaviour was followed in a cohort of cooperatively breeding white-throated magpie-jays from fledging through to dispersal. Young jays approached adult levels of foraging proficiency within 1 year of fledging. During their first year of age, young jays provisioned nests as helpers at a lower rate than did older individuals. No improvement occurred during that first year, however, suggesting that lower provisioning was the result of other factors than the lack of foraging or nesting skills. Natal dispersal was extremely sex-biased: males dispersed between 4 and 23 months of age, but females remained in their natal group. Male dispersal coincided with both the maturation of foraging skills and the start of a breeding season. Males from larger groups dispersed at an earlier age than those from smaller groups. Therefore, although offspring must associate with parents during some minimum period to acquire skills, the decision of whether and when to disperse from the natal territory is determined by other factors in the white-throated magpie-jay.

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In many species, offspring that appear to have reached physical maturity delay dispersal and help parents breed. The conventional view is that delayed dispersal is a result of ecological constraints that limit the dispersal opportunities of young (Emlen 1991). Most debate on the evolution and maintenance of cooperative breeding has centred on the relative importance of direct benefits of philopatry (e.g. access to territory resources, increased survivorship, increased probability of territorial inheritance) versus indirect fitness benefits from augmenting the production of kin (Brown 1987; Emlen 1991; Koenig et al. 1992).

One additional direct benefit of philopatry, which also predicts the age of natal dispersal, has been termed the skill hypothesis (Brown 1987). This hypothesis proposes that offspring are constrained to remain with parents until they have become proficient in behaviour necessary for successful dispersal and independent breeding (Lack

1968; Brown 1987; Koenig et al. 1992). The skill hypothesis is a possible explanation for the occurrence of delayed dispersal if three conditions are met. First, offspring must show improvement in 'skills' (e.g. foraging success, offspring provisioning, predator detection) throughout the period they remain with parents. Second, they must disperse as they approach adult proficiency. Third, those individuals that disperse first from a cohort should have reached adult proficiency earlier than those that delay dispersal. If the timing of dispersal is variable due to natural manipulation, however (e.g. death of parents, ejection from the territory), or experimental removal from parents, those who remain with parents longer must become more skillful than those who are forced to disperse early.

If offspring remain philopatric after reaching adult proficiency, or if dispersal occurs whenever a reproductive opportunity occurs, then other direct benefits of philopatry also influence the timing of dispersal. The need to learn skills may provide a minimum period that offspring must associate with parents, but other factors influence the timing of dispersal in this case. If all the necessary conditions for the skill hypothesis are present,

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however, one can only conclude that skill learning is one factor that is presently maintaining delayed dispersal. Prolonged philopatry may have evolved as a necessary adaptation to slow behavioural maturation. Alternatively, delayed dispersal may have first arisen because of other ecological and social constraints, and slow behavioural maturation evolved in response (see Discussion; Lawton & Lawton 1986; Koenig et al. 1992).

Numerous studies have shown an association between slow maturation of foraging skills and delayed breeding in species whose offspring disperse rather than remain with parents (Brown 1987; Wunderle 1991). Among species in which offspring delay dispersal, however, only a few studies demonstrate one of the conditions necessary to support the skill hypothesis, but none shows two or all three conditions. Brown jays, *Cyanocorax morio*, and bell miners, *Manorina melanophrys*, for example, improve at nest provisioning and other nesting behaviour while assisting parents, but continue to delay dispersal and breeding after reaching adult proficiency (Lawton & Guindon 1981; Lawton & Lawton 1985; Poiani 1993). White-winged coughs, *Corcorax melanorhamphus*, require 5 years to acquire adult foraging skills but remain in their natal group after reaching adult foraging proficiency, perhaps because several individuals are required to care for the slow-developing fledglings (Heinsohn 1987, 1991, 1992; Heinsohn et al. 1988).

The white-throated magpie-jay is a conspicuous, raucous bird that inhabits highly seasonal tropical dry forest and pasture in Central America (Skutch 1953; Langen 1994). Magpie-jays defend group territories in which one or two females breed while other members provision and defend offspring. Floater males also occur, who associate with members of several groups but provide little assistance during breeding (Langen, in press a). Magpie-jays have a broad diet, use various techniques for finding and harvesting food, and probably use social cues while foraging (Langen, in press b).

I observed the ontogeny of foraging, nest provisioning and other behaviour patterns from fledging through to natal dispersal among a cohort of magpie-jays. With these data, I examined whether maturation of skills is a sufficient explanation for the timing of dispersal. I also compared nest provisioning with foraging proficiency to determine whether the rate of

provisioning reflects foraging skill or differences in motivation that are correlated with age.

METHODS

Study Site and Population

This study was performed from July 1992 to August 1993 at Santa Rosa National Park, Guanacaste Conservation Area, Guanacaste Province, Costa Rica (10°50'N, 85°37'W; see Langen 1994, for a complete description of the site and characteristics of focal groups).

I marked nestlings from 14 groups with unique combinations of coloured plastic and aluminum leg bands at about 10 days post-hatching. During July 1992, 11 nestlings fledged from four groups within a period of 11 days (Table I). These individuals were treated as the focal cohort for the detailed study of skill maturation. I studied 24 additional known-aged fledglings from 10 other groups less intensively. Data on the transition to independence, morphology, nest provisioning and dispersal include these additional individuals.

Ontogeny of Foraging Skills

During the first 2 months after fledging, I made behavioural samples of focal individuals approximately twice weekly. After 2 months, I continued to sample the behaviour of each focal individual at intervals of 2 weeks or more frequently. A sample lasted for a cumulative minimum of 30 min (timed only when the animal was in sight) and up to 60 min. Magpie-jays are relatively tolerant of humans, so most observations could be made at a distance of 10–25 m from the birds for long continuous periods.

During these samples, I recorded whether a focal subject was foraging versus performing another activity. I defined foraging as scanning the environment while perched, hopping through vegetation or on the ground and manipulating substrates or handling prey. Flying during periods of these activities was also considered foraging. I noted each food item that the focal bird harvested. Most food items were identifiable: fruit to species, and arthropods to order or family. These data permitted me to calculate harvest rate (the number of items harvested per min of foraging time) for different kinds of food items. I also counted the number of begging calls made by the

Table I. Individuals in the focal cohort followed during this study

Group	Individual	Date hatched (in June 1992)	Date fledged (in July 1992)	Sex	Dispersed
Comedor	BO/PiM	13	5	F	—
	PG/OM	13	5	M	April 1993
	RPi/CM	13	5	M	January 1993
Casona	RC/PiM	19	13	F	—
	CO/RM	19	13	M	March 1993
Aviary	CP/WM	20	14	M	February 1993
	OO/OM	20	14	M	May 1993
	PiPi/PiM	20	14	F	—
	CC/CM	20	14	M	November 1992
Caja 2	PPi/PiM	23	16	F	—
	BC/CM	23	16	M	*

'Dispersed' represents the date of final disappearance from the natal group.

*This individual left its natal group for a period but subsequently returned.

focal individual and all instances that it was fed by other group members. On the same day or the following day, I observed the behaviour of an adult (age greater than 2 years) in the same manner as the focal fledgling. By sampling fledgling and adult foraging behaviour during the same period, I was able to compute relative foraging rates, controlling for temporal variation in food abundance.

Diet

While observing groups, I also recorded any food harvested by individuals other than the focal individual. Although ad libitum sampling can be biased towards conspicuous items, a comparison of the diet profiles provided by these data and diet profiles derived only from focal foraging samples were very similar. Because the focus of this study was behavioural rather than ecological, I later classified food items based on the behaviour used to capture and process them instead of splitting diet items to the greatest number of exclusive categories (Remsen & Robinson 1990; Sherry 1990). I later classified food items as caterpillars (the larvae of Lepidoptera), orthoptera (grasshoppers, crickets and katydids), other arthropods (e.g. insects and spiders), small fruit (berries and other fruit that can be swallowed whole with minimal processing), acacia (fruit of *Acacia collinsii* and *A. cornigera*, which require special harvesting skills because of stinging ants), large fruit (which required extensive handling), cocoons

(Lepidoptera pupae and spider egg masses), wasp nests (paper nests of polistine Hymenoptera), or miscellaneous (mostly human garbage).

Nest Provisioning

In 1992 and 1993, I collected data on nest provisioning of the breeding female(s) and nestlings during the long (February–July) nesting season. For 90 min per morning, I observed jay nests through spotting scopes at a distance of 20–75 m, depending on group members' tolerance of disturbance. I recorded all feeding visits, the identity of each provisioner, and the type of food provisioned during these samples. I calculated provisioning rate as the number of feeding visits per h.

Physical Measurements and Sexing

I weighed and measured all captured jays. Body measurements included length of the wing chord, tail, tarsus and beak, and weight. I also noted plumage and colour of the inner beak. Although most captured jays were unbanded and hence age was only approximately known (see below), fledged nestlings were recaptured as chance permitted. Young jays were caught and measured no more than once during their first year.

For all uncaptured as well as captured individuals, I made careful notes of plumage patterns. I sexed adult jays using sexually dimorphic plumage characters (Langen, in press a). Fledglings

moulted into adult plumage by 4 months of age and could then be sexed. Unbanded individuals were identifiable from unique plumage markings.

Statistical Analysis

To describe how behavioural and morphological measures converged on adult values with age, I performed asymptotic non-linear regressions (Draper & Smith 1981; Motulsky & Ransnas 1987; Juliano 1993). As a standard measure of 'maturation' (the asymptote), I calculated the predicted age (from the regression equation) that was required to reach 95% of the asymptotic value of the dependent variable (T_{95}). Parametric statistical tests were used whenever possible, and all variables were transformed as needed to meet the requirements of normality and homoscedacity. Otherwise, non-parametric statistical tests were used. Means and standard errors are reported throughout this paper.

RESULTS

Transition to Independent Foraging

Nestling magpie-jays fledged 23 days after hatching (22.9 ± 0.9 , range 18–25, $N=7$ nests). At fledging, young had distinctive immature plumage and beak gape coloration that remained until termination of adult provisioning (see Madge & Burn 1994, for an illustration). Until 18 days after fledging, young jays perched silently in thick vegetation and rarely interacted with other former nestmates. They made few loud begging calls to solicit feedings. Provisioning visits by adults were furtive and brief. The young birds were very poor fliers at this age and scrambled awkwardly along branches. Offspring survivorship was, not surprisingly, lowest during this period (1 month survivorship = 0.80 ± 0.081 , $N=25$; Langen, in press a).

Behaviour changed radically at about 18 days. Fledglings began producing loud begging calls, often from conspicuous perches, to solicit feedings by adults (Fig. 1; first day of >50 begs per h: 18.5 ± 1.79 , range 4–35, $N=22$). These calls were easily locatable broad-band sounds which I could detect from over 100 m.

Whether these calls were energetically costly is unknown, but it is likely that they attracted predators. For example, collared forest-falcons,

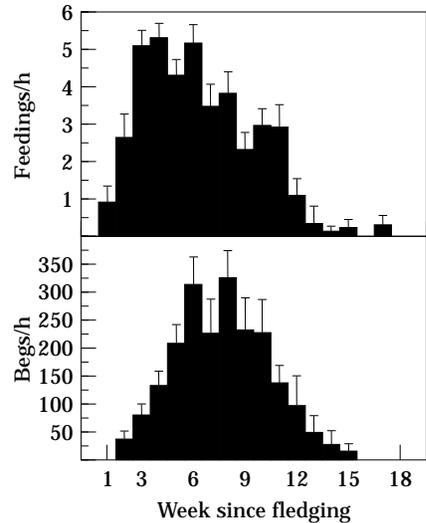


Figure 1. The mean number of feedings per h and begs per h each week during the first 18 weeks post-fledging for all sampled fledglings (N per week = 19 ± 3.9).

Micrastur torquatus, bird-eating hawks that hunt by stealth, were more frequently mobbed by groups at this time (6 of 168 sample mornings when begging young were present, 0 of 137 without; Fisher's exact test: $P < 0.05$). This apparent increase in the frequency of hawk encounters might have occurred because of more group movement or because adults had greater motivation to mob when young were present. There was no significant increase, however, in predator mobbing of all other threats, primarily mammals and snakes which were not as likely to follow foraging jays (11 of 168 sample mornings when begging young were present, 12 of 137 without; Fisher's exact test: $P > 0.5$). The only incident of predation that I ever witnessed away from a nest, in fact, was the killing of a begging fledgling by a forest-falcon.

Begging continued until 71 days post-fledging (70.9 ± 4.00 , range 52–96, $N=17$) and peaked around day 41 (Fig. 1; 41.6 ± 2.74 , range 15–76, $N=29$). Young were fed at a maximal rate around day 30 (Fig. 1; mean peak feeding day: 30.2 ± 2.13 , range 16–61, $N=29$). Feeding increased significantly with increasing beg rates but decreased (per individual) when there were more same-age siblings (Langen 1994). Evidence of parent-offspring conflict existed in the form of a significant difference between the age of peak

feedings and the age of peak begging: in most cases peak beg rate occurred after peak feeding rate (17 after, seven before and five ties; Wilcoxon signed rank test: $T=35$, $P<0.001$). Begging terminated at 76 days post-fledging (76.4 ± 2.98 , range 52–96, $N=16$).

At the time begging commenced, fledglings also began to interact with their former nestmates. I observed behavioural exchanges that can be interpreted as 'play' (Ficken 1977; Gaston 1977; Zahavi 1990) from about the third to the 12th week after fledging. For example, fledglings pursued each other in repetitive rapid flight around a tree in which adults were resting. They would also present a twig, nut or leaf to a sibling, which produced responses of tugging, chasing the possessor or passing the object back and forth. Siblings often squabbled, which involved piloerection, soft hissing vocalizations and pecking or biting. Nevertheless, reciprocal allopreening also frequently occurred.

Within 1 week of the onset of frequent begging, the fledglings began to follow foraging adults. They mobbed or chased adult group members while begging at high rates and attempted to steal food if not immediately fed.

During the same period that fledglings were pursuing adults, they also began the exploratory behaviour patterns that led to independent foraging (first foraging day: 20.7 ± 1.47 , range 12–39, $N=23$). Initially these exploratory behaviour patterns, such as breaking twigs, stripping bark or shuffling through leaves, resulted in few food items. They dropped many items or attempted to process non-food including nuts and old feathers (Fig. 2). The first successful harvest of food occurred about 1 week after the initiation of foraging behaviour (first harvest day: 27.4 ± 1.72 ; range 14–48, $N=27$). Fledglings began to harvest fruit before harvesting the first arthropod (first fruit harvest day: 29.7 ± 1.86 ; range 14–48, $N=26$; first arthropod harvest day: 35.3 ± 2.77 ; range 18–69, $N=24$).

Fledglings were also remarkably non-neophobic. Unlike adults, they entered traps repeatedly and came much closer to observers. They did not react to predators until parents gave alerting calls. Until 2 or 3 months post-fledging, they did not participate in appropriate mobbing behaviour.

After age 30 days post-fledging, birds markedly increased the time devoted to manipulating sub-

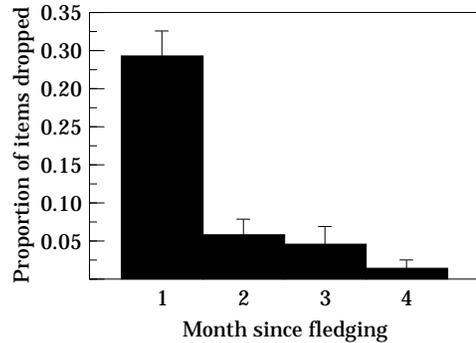


Figure 2. The proportion of all harvested food items that were dropped before being completely eaten during the first 4 months of foraging by fledglings of the focal cohort ($N=4$ groups).

strates and searching for food (see Foraging). By 3 months, young jays obtained all food by harvesting it themselves (last day fed by adults: 70.9 ± 4.00 , range 48–110, $N=17$). Rather than search randomly, however, they focused attention on locations and substrates where adults were foraging. Typically, a fledgling flew to an adult and begged if the adult had harvested a food item or was otherwise actively foraging. The adult did not necessarily feed the young individual, but usually left the location. The fledgling then began foraging at that site. These displacements were not accompanied by aggressive signals associated with dominance interactions such as occurred in similar encounters between adults. Although this pattern of foraging was most prevalent during the second and third months after fledging, I recorded instances up to 7 months of age.

Foraging

In the following sections, I document how members of the focal cohort improved towards adult proficiency in three components of 'foraging success': diet, harvest rate and time devoted to foraging.

Diet

I compared the diet of adults and fledgling cohort members over four periods which correspond to seasonal changes in food availability (August, middle wet season, 1 month post-fledging; September–December, late wet season,

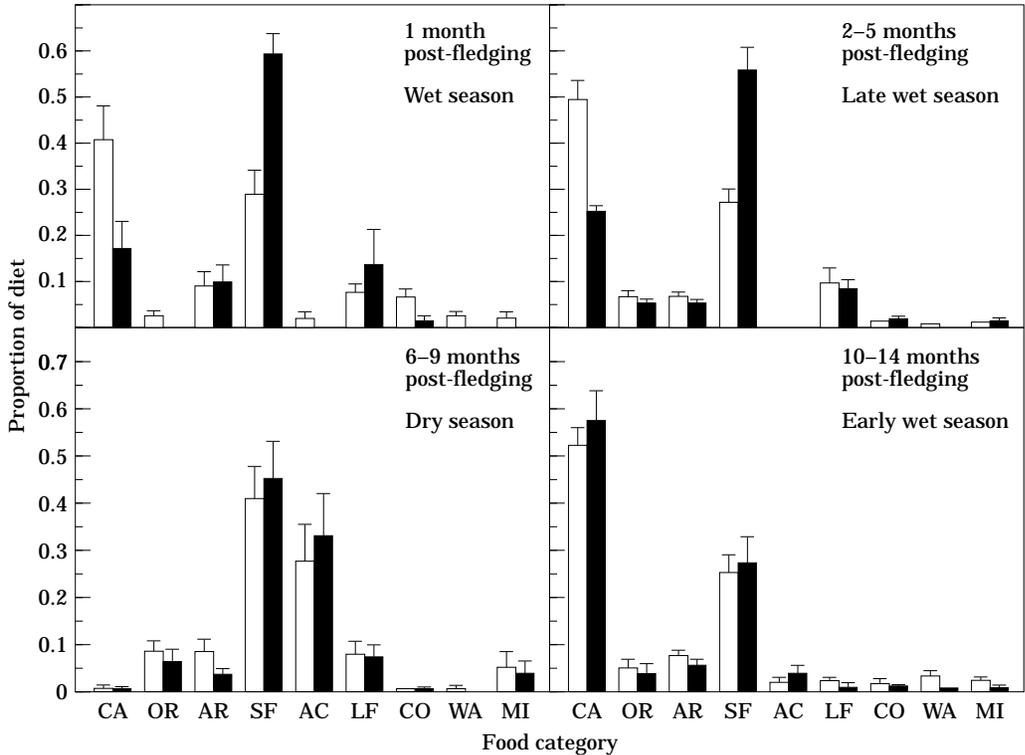


Figure 3. The diet of adults (□) and the fledgling cohort (■) during four periods, based on all food records. CA=caterpillars, OR=orthoptera, AR=other arthropods, SF=small fruit, AC=acacia, LF=large fruit, CO=cocoons and arthropod egg masses. WA=wasp nests, MI=miscellaneous.

2–5 months post-fledging; January–April, dry season, 6–9 months post-fledging; May–August, early wet season, 10–14 months post-fledging). The diets of the fledgling cohort and adults were initially very different but converged through time (Fig. 3). To compare the diets of first-year and older birds statistically, I performed chi-squared contingency tests for each group during each time period. I lumped diet categories, when necessary, to attain sufficient sample sizes for comparison and examined post-hoc tests to identify diet categories that were most different between age classes. I analysed each group separately to control for dietary differences between groups.

During the first two time periods (1 month post-fledging, 2–5 months post-fledging), diets were significantly different between the fledglings and adults in all four groups. Fledglings harvested relatively fewer arthropods and more fruit. During the dry season (6–9 months post-fledging), significant differences remained between the age

classes in two of the four groups. In these, juveniles harvested relatively fewer orthoptera and miscellaneous arthropods than adults. Finally, when the fledgling cohort was 10–14 months of age, significant differences in diet remained for only one group. Juveniles continued to harvest relatively fewer orthoptera and other arthropods.

Although the diet of cohort members was generally similar to that of adults by 1 year of age, the skills to harvest rare, difficult items could take longer to acquire. Wasp nests are one item that appeared to require special skills: individuals had to fly rapidly to the nest, grab with the beak the nest's pedicel and fly away from the pursuing wasps. I observed many instances where individuals were unsuccessful. I compared the number of individuals who successfully harvested wasp nests during the last period (cohort ages 10–14 months), for those individuals with over 15 feeding observations; mean feeding observations per individual=32.6 (cohort), 24.2 (adult). Significantly

fewer cohort members harvested wasp nests than adults (0 of 5 cohort members, 4 of 5 adults; Fisher's exact test: $P < 0.05$).

Harvest rate

One direct measure of the maturation of foraging skills is the change in harvest rate (items per unit time) with age. Where seasonality is as pronounced as in the Costa Rican dry forest, temporal variation in food abundances make the simple comparison of harvest rate with age highly misleading, however. To detect improvement in harvest rate, I used a measure that scaled harvest rate of a focal to that of adults at the time of the sample:

$$\text{Relative harvest rate} = \ln((\text{individual's harvest rate} + 1) / (\text{median adult harvest rate} + 1))$$

All samples of focal cohort members in which an individual foraged at least 5 min were included. Median adult harvest rate was based on all adult foraging samples over 5 min duration the week of the focal sample or the average of the sample medians of the two adjacent weeks when there were no adult observations the sample week.

Because diet changed with age from relatively more fruit to relatively more arthropods, I performed separate regressions on total harvest rate (all harvested food items), fruit harvest rate (small fruit, large fruit and acacia) and arthropod harvest rate (caterpillars, orthoptera, miscellaneous arthropods, wasps' nests and cocoons). For each analysis, I initially performed an ANCOVA using individual as the factor. Because neither the interaction term (testing for differences in slopes or rates of learning) nor the main effect (testing for consistent differences in harvest rate between individuals) was significant, I pooled observations for all 11 fledglings. I then performed asymptotic regressions (where the asymptote = 0) using the equation:

$$\text{Relative harvest rate} = \alpha e^{(\beta \text{age})}$$

Total harvest rate reached 95% of the asymptote (adult harvest rate) at 152 days post-fledging (Fig. 4). The harvest rate of fruit was equal to that of adults from the initiation of foraging. The harvest rate of arthropods reached 95% of the asymptote at 160 days post-fledging. Therefore, magpie-jays required about 6 months to reach a

mature food harvest rate, and most of the increase in harvest rate was due to improved harvesting of arthropods.

Search time

If young jays are less proficient foragers, one prediction is that they must either receive supplemental provisioning from adults or spend more time foraging. I compared changes in the proportion of time spent foraging during focal samples with age. For the same reasons as the analyses of harvest rate, I calculated foraging time relative to that of adults during the same period using the formula

$$\text{Relative foraging time} = \ln((\text{proportion of sample focal foraged} + 1) / (\text{median proportion adults foraged} + 1))$$

I included all focal samples. As in the analyses of harvest rate, I based the median proportion of time adults foraged on all adult samples the week of the focal sample or the average of the sample medians of the 2 adjacent weeks when there were no adult observations that week. I again initially performed an ANCOVA using individual as the factor. Because there was no significant effect of the factor, meaning that individuals did not significantly differ in foraging time when age was controlled, I pooled all individuals for the subsequent analysis.

A three-parameter non-linear regression model fitted significantly better than the two-parameter asymptotic regression model used in the other analyses ($F_{1,241} = 45.5$, $P < 0.001$). This model,

$$\text{Relative time foraging} = (c + a \text{Age}) \beta^{\text{age}}$$

produces a curve that approaches an asymptote of zero (where cohort time foraging = adult time foraging), overshoots the asymptote, and then approaches it from the other direction (Fig. 5). The shape of this model is reasonable, given the ontogeny of foraging behaviour. Fledglings spent proportionately less time foraging than did adults for the first 75 days post-fledging. This result corresponded to the period when they were provisioned by adults. From about day 75 post-fledging, they spent more time foraging than adults. This was the period when they were less proficient foragers but were no longer provisioned. The time devoted to foraging then gradually declined as foraging skills

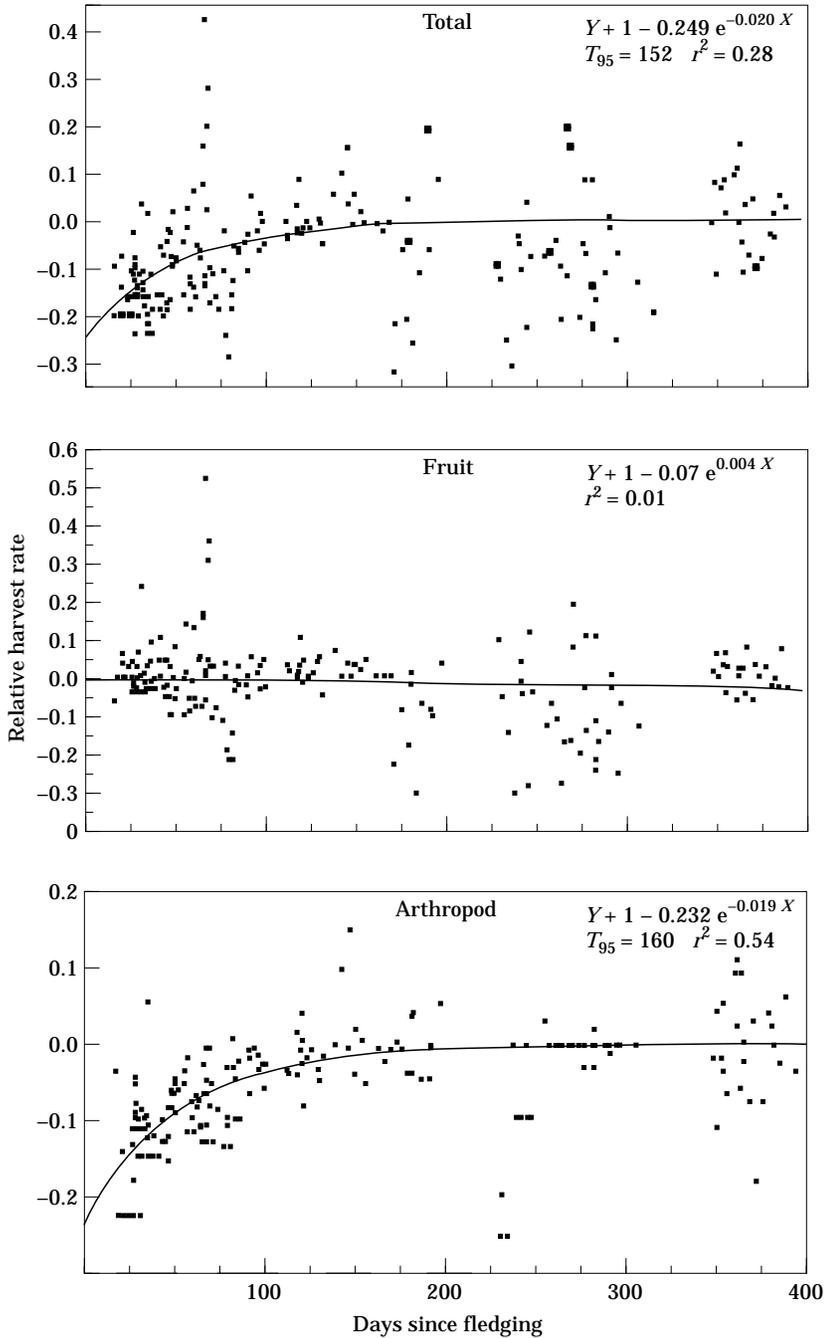


Figure 4. Improvement in harvest rate of food items with age (total: $F_{2,204}=17.10$, $P<0.001$; fruit: $F_{2,204}=1.63$, $P>0.20$; arthropods: $F_{2,204}=80.15$, $P<0.001$). Each point represents one focal sample of a foraging cohort member (see text for details of the method used to calculate the relative rate). Negative values indicate samples where focals foraged less than adults, positive values indicate samples where focals foraged more, and zeros indicate samples where adults and juveniles had equivalent harvest rates.

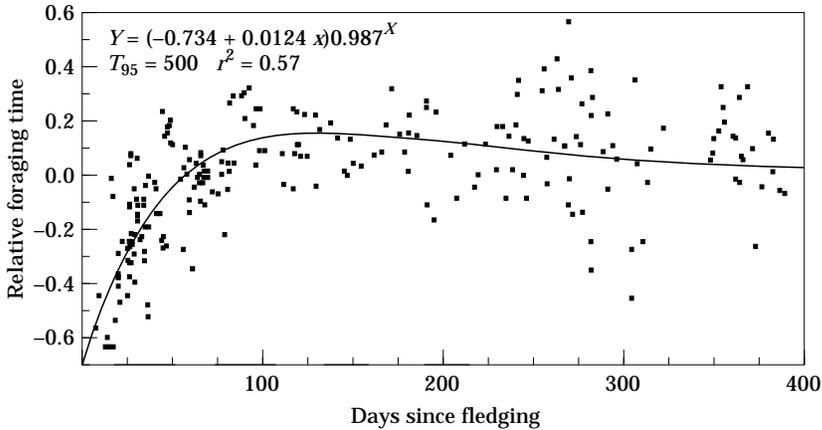


Figure 5. Change in the relative proportion of time spent foraging with age for the focal cohort ($F_{3,241}=104.75$, $P<0.001$; see text). Negative values indicate samples where focals foraged less than adults, positive values indicate samples where focals foraged more, and zeros indicate samples where adults and juveniles foraged an equal proportion of time.

improved. Although I did not collect data over a long enough period to be precise, the model implies that young jays require up to 16 months to reduce the time spent foraging to that of adults.

Physical Maturity

Improvement in foraging success may have been due, in part, to physical maturation (Marchetti & Price 1989). I examined differences in physical characteristics of all known-aged jays less than 1 year post-fledging and adults from measurements of captured individuals. Because white-throated magpie-jays are somewhat sexually dimorphic (males are 3% heavier and have 4% longer tarsi), I scaled young relative to the adult mean of their sex and non-linear regressions performed.

Tarsus length, an indicator of skeletal size, was equal to adult size at fledging ($F_{2,23}=0.26$, $P>0.5$). Beak length attained 95% of adult size at 3.9 months post-fledging (Fig. 6). Because the beak is essential for capturing and processing food, some of the improvement in foraging skill observed over the first few months may have been the result of growth (Marchetti & Price 1989; Desrochers 1992).

Fledglings averaged $90 \pm 1.2\%$ of adult weight during their first year ($N=35$). No significant increase in body weight was recorded during the

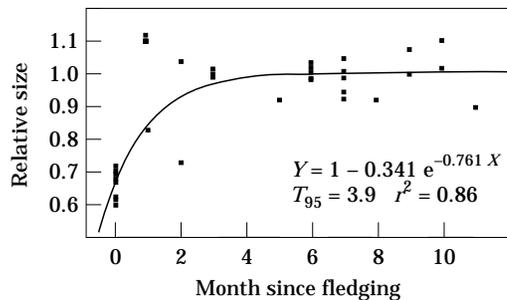


Figure 6. Growth of beak length with age (beak: $F_{2,34}=96.48$, $P<0.001$). Values less than 1 indicate samples where individuals had relatively smaller beaks than the mean adult length, values greater than 1 indicate samples where individuals were larger, and values of 1 indicate samples where the individual had a measurement equal to the adult mean.

period, however (regression of age on body weight, $r^2=0.005$, $P>0.5$), which was probably the result of a poorer diet, but differences in energy expenditure may also have contributed. Unfortunately, I have too few measurements of known-aged individuals after 12 months to track longer-term changes in weight with age.

Some species of New World jays change plumage and beak colour with age (Hardy 1973; Lawton & Lawton 1986; Peterson 1991). There were no apparent plumage or outer beak colour differences between juvenile and adult magpie-jays

after the first moult at 3–4 months post-fledging. Inner beak colour, however, did change with age. The colour change progressed from the base to the tip of the beak in the following order: bright red > pink > white > black. Throughout the first year, the inner beak colour was bright red to pink. Old birds (greater than 4 years) typically had nearly black inner beaks with some white near the tip.

Breeding Skills

Some jays were physiologically capable of breeding during the first breeding season after fledging (8–14 months post-fledging). For example, one female mated with a floater male at 11 months post-fledging but did not nest. Males who dispersed from their natal group during the first breeding season were observed courting females, albeit unsuccessfully. In another study conducted on the same population, three of six laparotomized females and three of five laparotomized males had fully developed gonads during the first breeding season (Innes 1992).

Because most of the skills necessary for successful breeding are not performed by non-reproducing individuals, it is difficult to determine the age at which these skills are acquired. For example, non-breeding group members that later participated in nest provisioning provided little assistance at nest building but probably had the necessary skills, since some female non-breeders occasionally built their own well-constructed nests on a territory after failing to assist the breeding pair at this task (Langen, in press a). The major breeding-related behaviour performed by offspring before dispersal, however, was provisioning breeding parents and their offspring.

I measured provisioning effort during the first breeding season and the second breeding season (19–26 months post-fledging) using data from nest watches and fledgling focal samples. I then calculated the expected number of feedings provided by each individual based on the expectation that all group members contributed equally. With these expectations, I performed chi-squared goodness-of-fit tests comparing the observed number of feedings made by an age class to the expected. I also noted the direction of the deviation (more or less than expected). I performed separate analyses on provisioning of the breeding female and of offspring, because the behaviour of non-breeding

group members differed between these two stages (Langen 1994). The number of feedings observed for a nest stage of a group was 24–410 ($\bar{X} \pm \text{SD}$ female provisioning: $N=88 \pm 35.4$; offspring provisioning: $N=206.8 \pm 20.8$).

During the first breeding season, all females but only two of seven males in the focal cohort provisioned the breeding female and offspring. Among those individuals that did provision, first-year birds in three of six groups provisioned the breeding female significantly less than did older individuals. In four of eight groups, first-year birds also provisioned offspring significantly less than expected. During the second breeding season, provisioning was in no case significantly less than that of older individuals. Provisioning was, however, significantly more to breeding females in three of five groups and to offspring in two of four groups. Therefore, if any improvement of provisioning skills occurs, it must be during the first breeding season.

I compared the proportion of feeding visits (juvenile provisions/total provisions) with age, including only those first-year birds who did provision throughout the breeding season. If young jays improved as helpers, this proportion should significantly increase. Instead, the proportion of feedings by first-year birds did not change significantly during the breeding season ($t = -1.3$, $df=8$, $P>0.2$; mean $r_s = -0.17 \pm 0.131$, $N=9$ individuals, based on 15–66 (mean=39.8) observation days per individual).

Not only may the rate of provisioning be lower, but the type of food items brought to the nest or fledglings may also vary in quality. Occasionally, I could identify the type of food brought to the nest ($N=57$ feedings among all groups observed). There was a significant difference in the type of food provisioned between the wet and dry seasons (arthropods versus fruit; Fisher's exact test: $P<0.001$). This difference reflected differences in adult diet: more fruit during the dry season and more arthropods during the wet season. There were no differences in food brought by adults versus first-year group members in either season, however (both seasons; Fisher's exact test: $P>0.1$; first year $N=18$, adult $N=39$). Provisioning 'mistakes' (e.g. refusal to give up an item brought to the nest, bringing inappropriate items such as sticks or leaves to nestlings) were made primarily by floaters rather than by young group members (Langen, in press a).

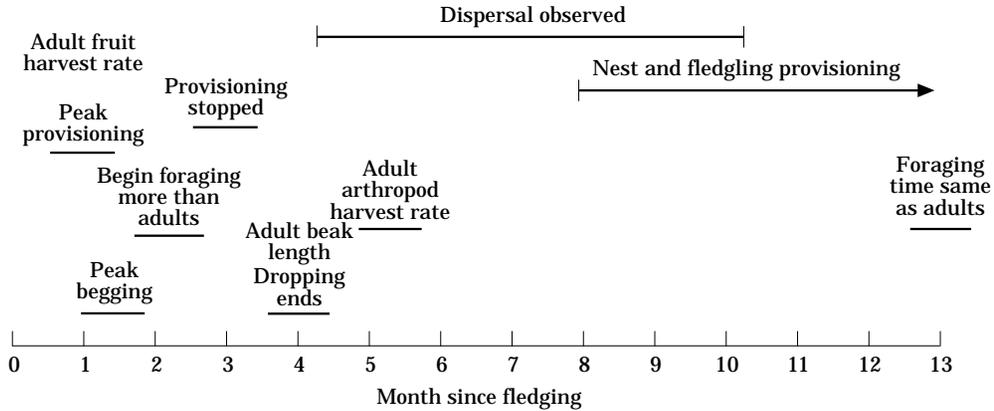


Figure 7. Summary of development during the first year of life.

Dispersal

About half of all offspring left their natal group during this study. Jays left their natal groups at 4–23 months of age, with the mode estimated at around 9 months. Most dispersal occurred during the dry season (January–April), coinciding with the start of breeding (Fig. 7). Dispersal was highly sex-biased. Six of seven males in the focal cohort dispersed between 4 and 10 months post-fledging (median age of dispersal = 7 months). No females dispersed. Among all fledglings that were sexed during the study, 14 of 17 dispersing individuals showed male plumage characteristics, and 13 of 14 philopatric individuals were sexed as females (Fisher's exact test: $P < 0.001$). Behavioural observations indicated that some individuals were misclassified; the bias was probably even more extreme. Of non-dispersers, four had remained in their natal group over 36 months by the end of the study (Langen, in press a). A similar sex bias was observed in another study where some individuals were sexed by laparotomy (Innes 1992). Male-biased natal dispersal is very uncommon in birds (Greenwood 1980; Greenwood & Harvey 1982); possible reasons for this unusual feature of the white-throated magpie-jay social system are discussed in Langen (in press a).

To determine whether the variation in dispersal ages of males in the focal cohort corresponded to variation in the rate of maturation of foraging skills, I compared the age of dispersal with arthropod harvest rate at 150 days post-fledging. I chose harvest rate of arthropods as an indicator of foraging ability, because this variable displayed

the most improvement with age. I estimated the harvest rate at 150 days from a regression of harvest rate on age for each individual. There was no significant negative correlation between individual harvest rate and dispersal age, indicating that skill acquisition rate did not determine the age of dispersal (Spearman rank correlation: $r_s = 0.29$, $N = 7$, $P > 0.4$).

On the other hand, there was a significant negative correlation between age of dispersal and total group size at the time of dispersal ($r_s = -0.78$, $N = 8$, $P < 0.05$). Related, non-independent measures of group size (e.g. number of same-age siblings, number of same-age male siblings, number of adults) had similar negative correlations with age of dispersal. Therefore, male offspring from larger natal groups dispersed at a younger age.

DISCUSSION

There are three principal findings in this study. First, offspring approached adult foraging proficiency by 1 year of age. Most improvement occurred in foraging on arthropods. For some rare dietary items, however, improvement occurred over a longer period than a year. Second, provisioning effort was less during the first breeding season after fledging than subsequently. No significant improvement in performance was observed during the first breeding season, however. Third, males dispersed from the natal group before 2 years of age, but females remained philopatric for much longer.

Timing of Dispersal and the Skill Hypothesis

As outlined in the Introduction, three conditions must be true if young delay dispersal because they lack skills: (1) offspring show skill improvement throughout the period they associate with parents, (2) dispersal coincides with maturity, and (3) association with parents increases the rate of skill acquisition or the range of skills acquired relative to individuals which are forced to disperse prematurely. Female magpie-jays remain in their natal groups as helpers long after reaching adult foraging and nest provisioning proficiency. Therefore, conditions (1) and (2) are not met, so the skill hypothesis is not applicable for them. Females stay and help for other reasons, such as pursuit of alternative reproductive tactics (Langen, in press a).

The skill hypothesis could be applicable to the timing of male dispersal, however. Male dispersal roughly coincided with the age of foraging maturity (Fig. 7). Nevertheless, there was considerable variation in the timing of dispersal, from 4 to 23 months of age. There was no significant association between the rate of maturation and dispersal age for males of the focal cohort. Instead, males in larger groups dispersed at earlier ages. Therefore, competition within groups may have affected the timing of dispersal. Most individuals who dispersed left during the dry season, when food was least abundant. Breeding also began during the dry season, however, so males may have dispersed to pursue mating opportunities. Permanent dispersal was preceded by visits to breeding females of neighbouring groups in several instances. After dispersal, males usually floated between nearby territories and were seen attempting to court females (Langen, in press a).

Therefore, the skill hypothesis is only qualitatively consistent with the timing of male dispersal in the white-throated magpie-jay. Some of the variation in dispersal age may be explained by competition within groups. The ultimate cause of dispersal is probably the opportunity to pursue reproductive opportunities rather than maturation of skills (Langen, in press a). Indeed, the association between maturation of skills and the timing of dispersal may go the other way around. Males may not need to be fully independent until the next breeding season, so skill development can be relatively slower than in species where young are forced to disperse earlier (Lawton & Lawton 1986; Koenig et al. 1992).

Nest Provisioning

Young non-breeders often provision less than older non-breeders or breeders (e.g. Lawton & Guindon 1981; Poiani 1993). They may provision less because they have not learned how to provision offspring adequately, because they are poorer foragers or because they are less motivated. The latter may occur because the direct benefits of provisioning are lower (e.g. establishing status in a group, opportunities for sneak matings or egg dumping; Rabenold et al. 1990; Zahavi 1990), or because the costs of provisioning are higher (e.g. reduced energy that can be allocated towards growth; Reyer & Westerterp 1985; Eden 1987; Heinsohn & Cockburn 1994). In principle, one can distinguish between the three hypotheses by observing how provisioning rate changes with experience. Provisioning should increase with experience if young need to learn provisioning skills. Provisioning should increase proportionally with improvement of foraging skills if foraging success is the main constraint on provisioning. If young provision less because of lower motivation, however, changes in provisioning effort should be unrelated to prior foraging or helping experience.

Most male white-throated magpie-jays performed little nest provisioning during the first breeding season after fledging. Among the females and few males which did provision, some provisioned significantly less during the first year of helping than older individuals. Nevertheless, there was no evidence of steady improvement in nestling provisioning during the first year. Young birds foraged nearly as proficiently as older jays by 1 year of age. They did not bring inappropriate food or make unusual mistakes. Therefore, although it is possible that first-year females were less skilled, it is more likely that they provisioned less because they were less motivated to help.

By the second breeding season, however, helpers (almost exclusively females) provisioned the same or more than older helpers and breeders. Innes (1992) also found that helpers in the second year provisioned more than any other age. She suggested that female helpers older than 2 years provision less because they pursue alternative reproductive tactics such as egg dumping or secondary nesting.

Skill Learning and Cooperative Breeding

Less is known about parental care after fledging than while offspring remain in the nest. Cooperatively breeding species, however, care for offspring 1.5–4 times longer than non-cooperatively breeding congeners (McGowan & Woolfenden 1990). Young of many cooperative breeders retain distinctive plumage, beak, skin or iris colour for an extended period which may also indicate immaturity (Hardy 1973; Lawton & Lawton 1986; Peterson 1991).

Offspring dependence may be prolonged because the cost to care-givers is relatively low. Per capita provisioning or vigilance costs, for example, may be lower when there are more individuals to share parental duties. Under this view, offspring remain dependent longer because adults do not choose to terminate investment (Brown & Brown 1984). Alternatively, a prolonged period of dependence may occur because offspring of cooperative breeders are inherently slower to develop. Because there is little evidence that physical growth is retarded (cf. Lawton & Lawton 1986), a longer period of dependence may be the result of taking longer to learn skills. Young in cooperatively breeding species may need to perfect specialized foraging behaviour (Heinsohn et al. 1988; Heinsohn 1991) or may be generalists and need to master many skills (Brown 1987).

Association with parents may provide two benefits. First, parental care may decrease risk while young are learning skills by providing a safety net in case of shortfalls and mistakes or by providing extra vigilance against predators. The decrease in risk permits young to invest more time in exploration and practice (Sullivan 1988; Heinsohn 1987, 1991). Second, adults may be a source of information by providing cues (Thorpe 1963; Werner & Sherry 1987). If adults serve as behavioural models and social learning is important for the acquisition of skills, the rate of learning may be higher and the range of skills acquired may be greater when young are able to remain near adults (Caro & Hauser 1992; Laland et al. 1993).

Magpie-jays provide extensive care to offspring during the first 3 months after fledging. Young are not forced to depend exclusively on self-feeding and can devote time to play and exploration of the environment. A juvenile will fly to an adult that is

actively foraging (e.g. tearing apart a bird's nest, tearing through a clump of leaves, pulling bark). The adult then flies off and the juvenile starts to forage. Initial efforts are often clumsy and inappropriate techniques are used (e.g. pecking rather than pulling bark). Following and 'scrounging' from adults may provide information about profitable foraging locations, substrates and food items. This may be why young jays become proficient at harvesting fruit before other food items: adults lead young to food patches, and fruit is conspicuous and easily harvested. To distinguish between the various mechanisms by which parents and other adults might facilitate acquisition of behaviour, however, will require experiments that measure the ontogeny of particular skills under different social conditions (Langen, in press b).

ACKNOWLEDGMENTS

S. Vehrencamp provided excellent support and advice throughout the study. I thank the staff of the Area de Conservacion Guanacaste, Costa Rica for permission to work in the wonderful park and for the many courtesies they performed during my stay. In particular, I thank R. Tiffer and R. Blanco in the research programme of the A.C.G. The paper was improved by the comments of J. Bradbury, T. Case, R. Gibson, J. Moore, R. Boyd, E. Fantino, S. Mitchell and the anonymous referees. G. Barker, W. Fonseca, G. Birch, S. Villarino, D. Hoffmann, K. Schoonmaker, K. Ward and J. Schalley worked extremely hard in the field to help gather these data. Financial support for the research was provided by an NIH Genetics Training Grant, the Tinker Foundation, Sigma Xi, the T.C. Schneirla Comparative Psychology Award, the American Ornithological Union, and NSF Research Grant IBN 9120789 (to S. L. Vehrencamp).

REFERENCES

- Brown, J. 1987. *Helping and Communal Breeding in Birds*. Princeton, New Jersey: Princeton University Press.
- Brown, J. & Brown, E. 1984. Parental facilitation: parent-offspring relations in communally breeding birds. *Behav. Ecol. Sociobiol.*, **14**, 203–209.
- Caro, T. M. & Hauser, M. D. 1992. Is there teaching in nonhuman animals? *Q. Rev. Biol.*, **67**, 151–174.

- Desrochers, A. 1992. Age and foraging success in European blackbirds: variation between and within individuals. *Anim. Behav.*, **43**, 885–894.
- Draper, N. R. & Smith, H. 1981. *Applied Regression Analysis*. New York: John Wiley.
- Eden, S. F. 1987. When do helpers help? Food availability and helping in the Moorhen, *Gallinula chloropus*. *Behav. Ecol. Sociobiol.*, **21**, 191–195.
- Emlen, S. T. 1991. Evolution of cooperative breeding in birds and mammals. In: *Behavioral Ecology* (Ed. by J. R. Krebs & N. B. Davies), pp. 301–335. Oxford: Blackwell Scientific Publications.
- Ficken, M. S. 1977. Avian play. *Auk*, **94**, 573–582.
- Gaston, A. J. 1977. Social behaviour within groups of jungle babblers, *Turdoides striatus*. *Anim. Behav.*, **25**, 828–848.
- Greenwood, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. *Anim. Behav.*, **28**, 1140–1162.
- Greenwood, P. J. & Harvey, P. H. 1982. The natal and breeding dispersal of birds. *A. Rev. Ecol. Syst.*, **13**, 1–21.
- Hardy, J. W. 1973. Age and sex differences in black-and-blue jays of Middle America. *Bird-Banding*, **44**, 81–90.
- Heinsohn, R. 1987. Age-dependent vigilance in winter aggregations of cooperative breeding white-winged choughs (*Corcorax melanorhamphos*). *Behav. Ecol. Sociobiol.*, **20**, 303–306.
- Heinsohn, R. 1991. Slow learning of foraging skills and extended parental care in cooperatively breeding white-winged choughs. *Am. Nat.*, **137**, 864–881.
- Heinsohn, R. 1992. Cooperative enhancement of reproductive success in white-winged choughs. *Evol. Ecol.*, **6**, 97–114.
- Heinsohn, R. & Cockburn, A. 1994. Helping is costly to young birds in cooperatively breeding white-winged choughs. *Proc. R. Soc. Lond. Ser. B*, **256**, 293–298.
- Heinsohn, R., Cockburn, A. & Cunningham, R. B. 1988. Foraging, delayed maturation and advantages of cooperative breeding in white-winged choughs, *Corcorax melanorhamphos*. *Ethology*, **77**, 177–186.
- Innes, K. E. 1992. The behavioral ecology and socio-biology of the white-throated magpie jay (*Calocitta formosa*) of Northwestern Costa Rica. Ph.D. thesis, Cornell University.
- Juliano, S. A. 1993. Nonlinear curve fitting: predation and functional response curves. In: *Design and Analysis of Ecological Experiments* (Ed. by S. M. Scheiner & J. Gurevitch). New York: Chapman & Hall.
- Koenig, W., Pitelka, F., Carmen, W., Mumme, R. & Stanback, M. 1992. Ecological factors and the evolution of delayed dispersal in cooperative breeders. *Q. Rev. Biol.*, **67**, 111–150.
- Lack, D. 1968. *Ecological Adaptations for Breeding in Birds*. London: Methuen.
- Laland, K. N., Richerson, P. J. & Boyd, R. 1993. Animal social learning: towards a new theoretical approach. *Perspect. Ethol.*, **10**, 249–277.
- Langen, T. A. 1994. Ecology, learning, and dispersal in the white-throated magpie-jay (*Calocitta formosa*). Ph.D. thesis, University of California, San Diego.
- Langen, T. A. In press a. The mating system of the white-throated magpie-jay *Calocitta formosa* and Greenwood's hypothesis for sex-biased dispersal. *Ibis*.
- Langen, T. A. In press b. Social learning of a novel foraging skill by white-throated magpie-jays (*Calocitta formosa*, Corvidae): a field experiment. *Ethology*.
- Lawton, M. F. & Guindon, C. F. 1981. Flock composition, breeding success, and learning in the brown jay. *Condor*, **82**, 27–33.
- Lawton, M. F. & Lawton, R. O. 1985. The breeding biology of the brown jay in Monteverde, Costa Rica. *Condor*, **87**, 192–204.
- Lawton, M. F. & Lawton, R. O. 1986. Heterochrony, deferred breeding, and avian sociality. *Curr. Ornithol.*, **3**, 187–222.
- McGowan, K. J. & Woolfenden, G. E. 1990. Contributions to fledgling feeding in the Florida scrub jay. *J. Anim. Ecol.*, **59**, 691–707.
- Madge, S. & Burn, H. 1994. *Crows and Jays: A Guide to the Crows and Jays of the World*. New York: Houghton Mifflin.
- Marchetti, K. & Price, T. 1989. Differences in the foraging of juvenile and adult birds: the importance of developmental constraints. *Biol. Rev.*, **64**, 51–70.
- Motulsky, H. J. & Ransnas, L. A. 1987. Fitting curves to data using nonlinear regression: a practical and non-mathematical review. *FASEB J*, **1**, 365–374.
- Peterson, A. 1991. Sociality and ontogeny of coloration in the blue-and-black jays. *Wilson Bull.*, **103**, 59–67.
- Poiani, A. 1993. Social structure and the development of helping behaviour in the bell miner (*Manorina melanophrys*, Meliphagidae). *Ethology*, **93**, 62–80.
- Rabenold, P., Rabenold, K., Piper, W. & Zack, S. 1990. Shared paternity revealed by genetic analysis in cooperatively breeding tropical wrens. *Nature, Lond.*, **348**, 538–540.
- Remsen J. V., Jr. & Robinson, S. K. 1990. A classification scheme for foraging behavior of birds in terrestrial habitats. *Stud. Avian Biol.*, **13**, 144–160.
- Reyer, H. U. & Westerterp, K. 1985. Parental energy expenditure: a proximate cause of helper recruitment in the pied kingfisher (*Ceryle rudis*). *Behav. Ecol. Sociobiol.*, **17**, 363–369.
- Sherry, T. W. 1990. When are birds dietarily specialized? Distinguishing ecological from evolutionary approaches. *Stud. Avian Biol.*, **13**, 337–352.
- Skutch, A. F. 1953. The white-throated magpie-jay. *Wilson Bull.*, **65**, 68–74.
- Sullivan, K. A. 1988. Ontogeny of time budgets in yellow-eyed juncos: adaptations to ecological constraints. *Ecology*, **69**, 118–124.
- Thorpe, W. H. 1963. *Learning and Instinct in Animals*. London: Methuen.
- Werner, T. K. & Sherry, T. W. 1987. Behavioral feeding specialization in *Pianroloxias inornata*, the 'Darwins finch' of Cocos Island, Costa Rica. *Proc. natn. Acad. Sci. U.S.A.*, **84**, 5506–5510.
- Wunderle, J. M. 1991. Age specific foraging proficiency in birds. *Current Ornithol.*, **8**, 273–325.
- Zahavi, A. 1990. Arabian babblers: the quest for social status in a cooperative breeder. In: *Cooperative Breeding in Birds. Long-term Studies of Ecology and Behaviour* (Ed. by P. B. Stacey & W. D. Koenig), pp. 104–130. Cambridge: Cambridge University Press.