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Movement and behavior of scarlet macaws (*Ara macao*) during the post-fledging dependence period: implications for in situ versus ex situ management

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Abstract

Knowledge of scarlet macaw (*Ara macao*) biology during the post-fledging period is limited, yet information about this important life stage is critical to developing effective conservation strategies. We used radiotelemetry to study the post-fledging movements and behavior of scarlet macaws from an isolated and threatened population in Costa Rica. Our results indicate that monitoring and protection of young macaws during the initial 14 days post-fledging is a critical conservation measure. We identify coastal mangrove as an important habitat for the species during the post-fledging period. Young scarlet macaws gradually developed flight and feeding skills, learned behaviors and movement patterns from their parents, and were integrated into social groups during the post-fledging period. Our results underscore the challenges facing management programs based on captive rearing and stress the importance of in situ conservation focusing on nest cavity management and protection in cooperation with local communities.

Keywords: Scarlet macaw; Radiotelemetry; Post-fledging period; In situ conservation; Costa Rica

1. Introduction

The scarlet macaw (*Ara macao*) is one of the most emblematic and recognizable bird species of the Neotropics. Previous studies of wild scarlet macaw populations have focused on habitat use, population dynamics, and reproductive ecology (Marineros and Vaughan, 1995; Nycander et al., 1995; Gilardi, 1996; Iñigo-Elías, 1996; Vaughan, 2002). Scarlet macaws are cavity nesters. A breeding pair typically produces two to three eggs per clutch (Abramson, 1995a), and a successful nest may fledge one, two, or rarely, three young (Munn, 1992; Nycander et al., 1995). The availability of suitable nest sites may limit population growth (Nycander et al., 1995; Vaughan, 2002), and like many Neotropical psittacines, scarlet macaw nests are subject to high poaching rates by humans (Marineros and Vaughan, 1995; Wright et al., 2001).

Given these potential limiting factors and the charismatic nature of the species, scarlet macaws have attracted the attention of conservationists throughout their range. In situ conservation efforts have attempted to increase reproductive output by protecting natural nests, providing secure artificial nest cavities (Nycander et al., 1995; Vaughan et al., 2003b), and working with local communities to reduce nest poaching (Vaughan et al., 2003a). Other projects have used a variety of ex situ methods, including removing wild-born chicks with high mortality risks from nests for captive rearing and later release into native habitats (Nycander et al., 1995; Nader et al., 1999) and reintroducing macaws confiscated in the pet trade or produced in captive breeding facilities (Bradshaw et al., 1996; Nader et al., 1999).

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Despite research emphasis on nesting ecology, information on scarlet macaw biology during the post-fledging period is limited. This period is an important time of continuing physical and behavioral development in the life cycle of altricial birds (Anders et al., 1998; Tyack et al., 1998; Wood et al., 1998). We used radiotelemetry to study scarlet macaws during the post-fledging period in Central Pacific Costa Rica. The objective of our research was to describe the movements, behavior, and social development of scarlet macaws during this little-known life stage. We discuss our findings in relation to current scarlet macaw conservation strategies and suggest that a better understanding of the post-fledging period can improve the effectiveness of conservation efforts for the species.

2. Methods

2.1. Study site

An estimated 330 macaws inhabit a 560-km^2 region of Central Pacific Costa Rica (Vaughan, 2002). Prior to Spanish colonization, this region consisted primarily of tropical forests in the dry to humid transition zone with small areas of premontane and tropical wet forests (Tosi, 1969). Currently, the landscape is dominated by agriculture and small (<40 ha) forest patches. Most remnant forest patches >200 ha are found within protected areas. The climate is warm (mean annual temperature 25–30 °C) and humid (2.5–3.3 m annual precipitation) with distinct wet (May–December) and dry (January–April) seasons (Coen, 1983; Herrera, 1986).

Our research was conducted in a 75-km^2 area of the Central Pacific region (Fig. 1a). The study area contained native forest patches used by macaws in three protected areas. Macaws nested and fed extensively in the primary and secondary forests of Carara National Park (5500 ha) and to a lesser degree in the privately owned Punta Leona Biological Reserve (300 ha). Coastal mangrove habitat in the Guacalillo Mangrove Reserve (1100 ha) was used by some macaws for nesting and by the majority of the population as a nocturnal roosting site. Macaws also fed and nested regularly in forest fragments on privately owned agricultural lands, and much of our work was conducted on cattle ranches, especially Hacienda Quebrada Bonita.

2.2. Study animals

During the 1995–1997 nesting seasons, we fitted eight nestlings from four nests with collar-mounted radio-transmitters (Model Al–2C; Holohil Systems Ltd., Ontario, Canada) approximately two to four days prior to fledging (Table 1). Transmitters were housed in a brass cylinder mounted on an adjustable band with a locking nut closure. Battery life was estimated at 52 weeks, and radiocollar weight was 30 g, approximately 3% of the body mass of a scarlet macaw fledgling.

2.3. Post-fledging movements

Macaws were tracked from the ground using a TR-2 receiver and RA-2A antenna (Telonics, Mesa, Arizona, USA). In 1995 and 1997, fledglings were tracked at least five days per week during the first 14 days post-fledging. Thereafter, they were tracked two days per week until day 42 (1995, 18 tracking days, 54 locations) and day 63 (1997, 23 tracking days, 141 locations). In 1996, fledglings were tracked more intensively: three to five days per week until day 97 (51 tracking days, 166 locations) with opportunistic sightings up to 343 days post-fledging. Each tracking day, at least one location per individual was recorded during each of three periods: early morning (06:00–08:30 h), daytime (08:31–15:30 h), and late afternoon (15:31–18:00 h). We chose these periods to identify when fledglings began making daily movements between nocturnal roosting sites and diurnal home ranges. When possible, macaws were visually sighted and their locations plotted on a 1:50,000 topographic map (Instituto Geográfico Nacional, San José, Costa Rica). When sightings were not possible, macaw locations were estimated using triangulation.

This research was part of a larger scarlet macaw conservation program, one aspect of which aimed at increasing the reproductive output of the population (Vaughan, 2002). Therefore, while our study was primarily descriptive, we did intervene to protect fledglings from predators by housing them in a protective cage overnight when we considered mortality risks to be high.

2.4. Post-fledging behavioral and social states

Because the movements of fledglings 961 and 962 were localized and occurred in relatively open habitats, we were able to observe their behavior in detail during the first 11 weeks post-fledging. After day 77, increased daily movements made it increasingly difficult to observe behavior.

Fledglings were located using radiotelemetry combined with auditory and visual cues. Once located, if conditions permitted, we recorded the fledglings' behavioral and social states using instantaneous scan samples of focal individuals (Altmann, 1974). Observation periods were 15-min bouts with behavioral data recorded every 60 s. If the sibling pair were <10 m apart, data were recorded for both with the scan moment offset by 10 s. If the subject flew away or became obscured by vegetation during the observation period, the session was terminated and data were discarded.

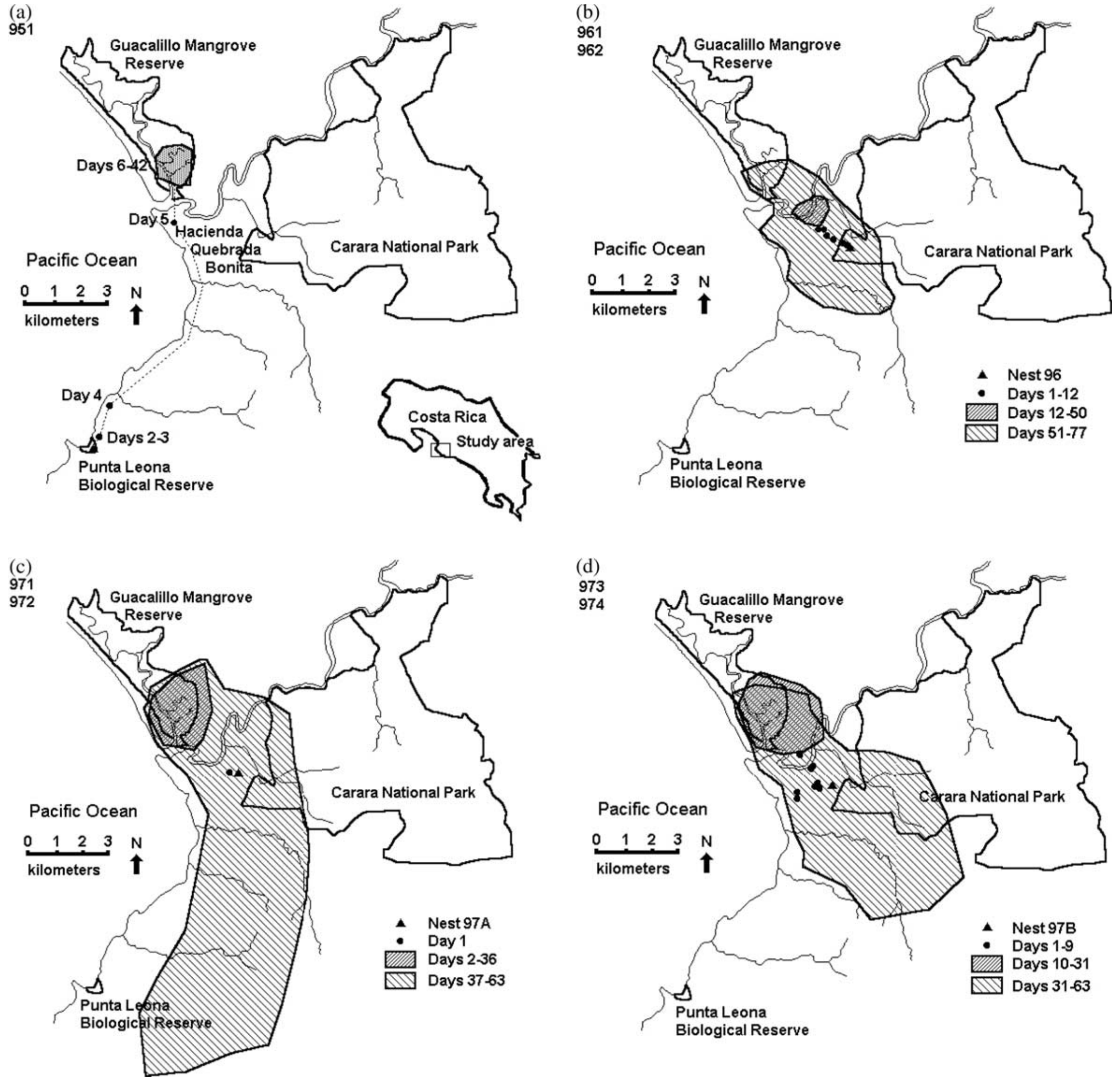

Fig. 1. Movement patterns of scarlet macaw fledglings in Central Pacific Costa Rica. Four nests, each producing two fledglings, were monitored during the 3-year study. Each map (a–d) depicts the movements of a single brood. "Days" is defined as the number of days post-fledging. The figure illustrates the three movement patterns exhibited by young macaws during the post-fledging period. During the first period (Days 1–12), fledglings remained within 1 km of the nest site. During the second period (Days 12–50), fledglings exhibited limited daily movements after an initial dispersal 1–12 km from the nest site. Three of the four broods spent the entire second period in the Guacalillo Mangrove Reserve. During the third period (Days 31–77), fledglings made daily movements between nocturnal roosts in the coastal mangrove and home ranges to the south and east. Variation in the duration of the periods in the figure legends reflects natural variation among broods.

For each instantaneous scan, one of six behavioral states was recorded. *Resting* described behaviors where the bird was sleeping, sitting quietly, or preening. *Manipulation* included behaviors where small branches or leaves were broken and maneuvered with the feet, beak, or tongue but no plant material was consumed. *Interaction with parents* described any physical contact between the fledgling and its parents, including feeding, preening, play, and beak-to-beak contact. *Interaction with sibling* described any physical contact between the fledglings, predominantly play and beak-to-beak contact. *Locomotion* included any short movements, either climbing or flying, within the observation area. *Foraging* described the consumption of seeds, fruits, or bark.

The social state of the focal individual was also recorded at each instantaneous scan. We considered a fledgling to be socializing with another macaw if the birds were perched within 30 m of one another and were exchanging vocalizations. Four social states were recorded: *alone*, *with sibling*, *with parents*, and *with unrelated macaws*. Social states were not mutually exclusive. We pooled data for both fledglings and calculated weekly averages for behavioral and social states.

Table 1
Nest site characteristics and fledging details for 8 radiocollared scarlet macaws in Central Pacific Costa Rica

Nest ID	Location	Habitat type (tree species)	Nest type	Animal ID	Hatch order/ clutch size	Date fledged	Minimum survival (days)
95	Punta Leona Biological Reserve	Riparian fragment (*Schizolobium parahybum*)	Natural	951	2/3	30-Apr-1995	42
				952	3/3	5-May-1995	1
96	Carara National Park	Primary forest (*Schizolobium parahybum*)	Artificial	961	1/2	20-May-1996	343
				962	2/2	22-May-1996	343
97A	Hacienda Quebrada Bonita	Pasture (*Ceiba pentandra*)	Artificial	971	1/2	25-Apr-1997	97
				972	2/2	28-Apr-1997	97
97B	Hacienda Quebrada Bonita	Pasture (*Aspidosperma spruceanum*)	Artificial	973	1/2	25-Apr-1997	97
				974	2/2	29-Apr-1997	97

*Macaw 974 was poached from another nest, recovered from poachers, and fostered in nest 97B.

3. Results

3.1. Fledging events

Immediately upon fledging (72–79 days old), macaws typically flew <100 m and perched in forest patches at the edge of open habitats. In 1995, this was in a riparian strip corridor overlooking a hotel complex; in 1996 in Carara National Park where primary forest meets a trail and administration area; and in 1997 in a forest fragment adjacent to pasture on Hacienda Quebrada Bonita. No fledgling returned to the nest cavity during the early post-fledging period.

Two macaws were weak flyers and fell to low perches during the initial 14 days post-fledging; both were the youngest of their brood. Fledgling 952 fell to the ground immediately after fledging. We returned it to the nest cavity; however, it departed the nest again the following afternoon and was killed by an unidentified small carnivore that night. Fledgling 962 fell to low branches (<2 m) several times during the first 14 days post-fledging. We protected this macaw from predators by housing it in a protective cage overnight on several occasions. By day 15, fledgling 962 had significantly improved muscle coordination and flight ability, and henceforth its movements and behavioral development closely resembled those of its elder sibling.

3.2. Post-fledging movements

We identified three periods of distinct movement patterns during the post-fledging period. During the first period, lasting 1–12 days post-fledging, macaws exhibited limited movements within a 1-km radius of the nest site. Some broods left the nest site almost immediately; fledglings 951, 971, and 972 spent a single day near the nest before flying to the Guacalillo Mangrove Reserve (Figs. 1a and c). Other broods showed fidelity to the nest site for several days. For example, fledglings 961 and 962 spent seven days within 250 m of the nest site before gradually dispersing to a riparian forest patch near the Tarcoles River (Fig. 1b). Likewise, after fledging on 25-Apr, fledgling 973 spent three days within 1 km of the nest in forest fragments on Hacienda Quebrada Bonita and an adjacent farm (Fig. 1d). On day 4, 973 flew 3 km to the Guacalillo Mangrove Reserve while 974 fledged and flew to a forest fragment 100 m from the nest. The following day, 973 returned from the Gaucalillo Mangrove Reserve with the parents to the forest fragment where 974 was located, and the siblings spent the next three days together on the farms before flying together to the mangrove on 4-May.

The second period began with a dispersal of 1–12 km from the nest sites and lasted 30–50 days post-fledging. During this period, fledglings exhibited restricted daily movements within relatively small areas (200–700 ha). Five of the seven fledglings that survived to this age (951, 971, 972, 973, 974) flew to the Guacalillo Mangrove Reserve (3–12 km from nest sites) within 10 days of fledging (Figs. 1a, c, d). Once in coastal mangrove habitat, the fledglings typically occupied small areas (<20 ha) for several consecutive days before moving to a different portion of their range. Fledglings 961 and 962 showed the same general pattern of limited movements within a small area; however, their activity center was located in a riparian strip corridor on Hacienda Quebrada Bonita (Fig. 1b). Over 80% of the locations for 961 and 962 during this period were from a small area (<5 ha) of riparian vegetation containing mature *Pithecelobium samaan* trees.

One fledgling disappeared during the second period. We were unable to locate fledgling 951 after day 42. We suspect its collar failed but cannot rule out dispersal outside of the study area.

The third period began when fledglings began making daily movements between nocturnal roosts in the Guacalillo Mangrove Reserve and daily activity centers to the south and east. During this period, ranges were large (>1000 ha). Daily movements were frequent and covered large distances, up to 15 km on single flights. All sibling pairs continued to exhibit highly correlated movements during this period. While fledglings 961 and

Table 2
Key events in the behavioral development of scarlet macaw fledglings 961 and 962 during the post-fledging dependency period in Central Pacific Costa Rica

Days	Observation
1	Chicks fledge; no post-fledging dependency on nest cavity
2–14	Brood split; Each fledgling within 250 m of nest site
14–28	Fledglings together during 50% of observations
12–50	Fledgling movements very limited; over 80% of locations within 5 ha area on Hacineda Quebrada Bonita
39	First observed physical interaction between siblings
39	First social contact with adult macaws other than parents
45	Peak in frequency of *manipulation* behavior
50	Increase in frequency and intensity of sibling play
51	Fledglings begin accompanying parents on daily flights to and from nocturnal roosts in Guacalillo Mangrove Reserve
57	First observation of chicks foraging independently
56–77	Fledglings in flocks of >10 individuals during 45% of observations
77	Behavioral observation terminated
78–97	Fledglings expand range south into Carara National Park and adjacent private lands; daily flight paths > 20 km
97	Radiotracking terminated
212	Opportunistic sighting with pair of adult macaws (presumed parents) at Nest 96; no nesting activity at Nest 96 in 1997
343	Opportunistic sighting of fledglings on Hacienda Quebrada Bonita with group of 12 macaws

962 spent most of their daytime hours within a few kilometers of their nest site (Fig. 1b), fledglings 971 and 972 were wide-ranging, moving up to 15 km south of roosts in the coastal mangrove each day (Fig. 1d).

3.3. Post-fledging behavior and social state

A total of 308 behavioral observation periods (28.0 ± 8.9, weekly mean $\pm$ S.D.) were compiled in 1996. Key events in the behavioral development of fledglings 961 and 962 are presented in Table 2. Both adult macaws provided parental care to the fledglings for the duration of the 11-week study. During the first two weeks post-fledging, fledglings spent 70–80% of their time alone and resting and about 20% being preened or fed by regurgitation by their parents (Fig. 2a). Fledglings were completely dependent upon their parents for food during the first eight weeks post-fledging. During this time, both parents visited each fledgling four to seven times daily. Fledglings were always fed and usually extensively groomed during visits lasting from 1 to 90 min. Beginning in third week, the proportion of time the fledglings spent together progressively increased, and a high proportion of the fledglings' daily activity budget was devoted to the manipulation behavior. A peak in the manipulation behavior preceded the first observation of independent foraging in week 9 (Fig. 2a).

Fledglings became increasingly social as the study progressed (Fig. 2b). Each fledgling spent most of the first two weeks alone, interacting only with its parents. After week 3, the sibling pair was frequently together, though we did not observe physical interaction between them until week 6. Beginning in week 5, a pair of adult macaws of unknown kinship occasionally accompanied the parents on visits to the fledglings. During week 8, frequency and intensity of play behavior between siblings (chasing each other while climbing among branches, sparring with their feet and beaks, and hanging upside down by the feet while beating each other with their wings) increased markedly. At the same time, there was a sharp increase in the amount of time spent with unrelated macaws as the fledglings began making daily movements in flocks of eight to 30 individuals between nocturnal roosts in the coastal mangrove and diurnal home ranges. However, we never observed fledglings interact physically with any macaw other than their parents or sibling.

4. Discussion

4.1. Radiotelemetry

Previous studies have employed radiotelemetry to study psitaccine ecology (Lindsey et al., 1991; Lindsey et al., 1994; Snyder et al., 1994; Meyers, 1996; Meyers et al., 1996), including Buffon's Macaw (*Ara ambigua*) in northeastern Costa Rica (Bjork and Powell, 1995). Our study is the first to use radiotelemetry to track free-ranging scarlet macaws. Radiotelemetry proved a useful tool for studying movements and behavior during the post-fledging period. The robust collar design prevented damage during social preening, and macaws manifested no apparent collar-related injuries during the study. Radiocollars did not appear to influence fledgling or parental behavior.

We recommend future radiotelemetry studies to improve knowledge scarlet macaw biology, especially during the post-fledging period. Increased sample sizes are needed to determine survival rates, to assess

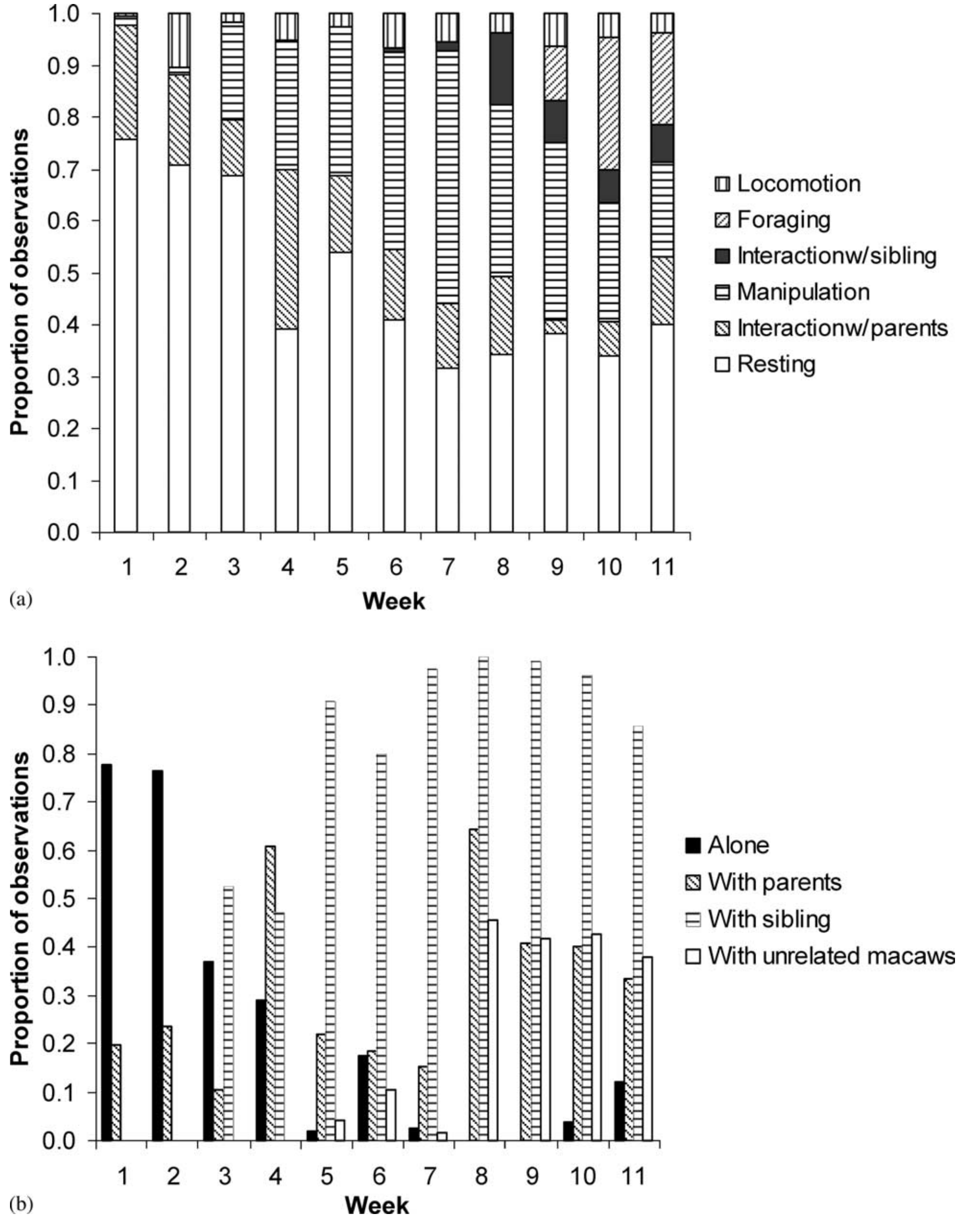

Fig. 2. Weekly behavioral budgets and social states of scarlet macaw fledglings 961 and 962. Behavioral states (a) were mutually exclusive, so proportions for all activities sum to 1.0 each week. Fig. 1a illustrates a peak in the manipulation behavior prior to the initiation of independent foraging and an increase in physical interaction among siblings during weeks 8–11. Social states (b) were not mutually exclusive (i.e., a fledgling observed with its sibling and its parents received a score for each category), so weekly sums exceed 1.0. (b) Fledglings' social interaction increased over time, first among the sibling pair and then with unrelated macaws.

variation in movements and behavioral development among broods, and to describe habitat use. We tracked macaws from the ground with only one researcher afield; this approach was successful for 60–80 days post-fledging, but monitoring for the full life of the transmitters would require greater resources than we had available. For future studies we recommend improved capacity to track animals, including simultaneous monitoring by multiple researchers, access to all-terrain vehicles, and periodic searches from aircraft.

4.2. Protection during the early post-fledging period

During the first 14 days post-fledging, two of the eight fledglings exhibited poor flight ability and muscle coordination and exposed themselves to predators by falling to low perches. Both were the youngest of their brood. Stunting of the youngest nestlings of a brood has been well-documented in captive settings (Abramson, 1995b), and the removal and hand-rearing second- and third-born nestlings has been an integral part of macaw conservation efforts in Peru (Nycander et al., 1995). Our results suggest that even when younger nestlings survive and fledge naturally, they may face higher mortality risks than elder siblings during the early post-fledging period. Observation of a fledging event may not be the appropriate metric for measuring nesting success, as is commonly assumed.

A key component of conservation efforts in our study area has been 24-h guarding of active nests by park personnel, volunteers, and paid local residents to curtail nest poaching. Protection of three to six nests in a concentrated area on Hacienda Quebrada Bonita costs approximately US$1500 for the three-month nesting season (Vaughan et al., 2003b). Currently, protection efforts are terminated when nestlings fledge; however, our findings indicate a potential need for continued vigilance during the early post-fledging period. If fledgling events are observed or the fledglings are radiocollared, the need for additional monitoring can be quickly determined based on behavioral observation. For example, some macaws flew up to 3 km the day after fledging while others could barely maintain a perched position.

Fledglings with poorly developed flight skills and muscle coordination may require up to 14 days of additional protection. We recommend 24-hr observation and assisting awkward fledglings by placing them in protective cages at night when exposure to predators is considered high. For nests that have already been guarded for three months, the cost of extending protection efforts into the post-fledging period is small given the high risk of mortality.

4.3. Importance of coastal mangrove habitat and privately owned lands

As the largest remnant of forested habitat in the region, Carara National Park is an important site for the conservation of the Central Pacific scarlet macaw population; however, our results highlight the value of lands outside of the national park. For instance, in addition to being a social roosting site for adult scarlet macaws throughout the year (Vaughan, 2002), the Guacalillo Mangrove Reserve was a very important habitat for scarlet macaws during the early post-fledging period. Given these observations, we believe that the Guacalillo Mangrove Reserve has special habitat value for this threatened population of scarlet macaws. Snyder et al. (2000) and Wiedenfeld (1994) indicate that the Central Pacific scarlet macaw population is of global significance because it represents the northernmost viable population of the subspecies *Ara macao macao*. While the Guacalillo Mangrove Reserve has been recognized as a national wetland reserve, its small size, isolation, and legal status make it more susceptible to degradation than a national park. We propose that the Guacalillo Mangrove Reserve warrants inclusion on the "List of Wetlands of International Importance" under the Ramsar Convention on Wetlands, an international agreement on wetland conservation to which Costa Rica is a signatory.

Our findings also indicate that economic land use for cattle production and scarlet macaw conservation are not mutually exclusive. Scarlet macaws are wide-ranging, have a diverse diet (Marineros and Vaughan, 1995; Nycander et al., 1995), and are highly intelligent and adaptable, characteristics that promote their persistence in mosaic landscapes. For instance, six macaws fledged from three nests in 1-km^2 of Hacienda Quebrada Bonita pasture with remnant mature trees in 1997, and over 80% of fledgling locations in 1996 occurred in Hacienda Quebrada Bonita forest fragments. Some cattle husbandry practices, such as leaving mature *Anacardium excelsum*, *Ceiba pentandra*, *Enterolobium cyclocarpum*, *Hura crepitans*, and *P. samaan* trees in pasture for shade and fruit for cattle and preserving woody vegetation along riparian corridors, benefit macaws. The owners of Hacienda Quebrada Bonita have been very supportive of the artificial nestbox program and protection efforts, and expanding cooperation with other private landowners in the region in a similar manner is key to the future management of this population.

4.4. Management implications of behavioral and social findings

Management of scarlet macaw nests at high risk of being poached has been a controversial issue in Central Pacific Costa Rica. Two basic approaches have evolved: an in situ approach based on reducing poaching through nest cavity management and environmental education (Vaughan, 2002; Vaughan et al., 2003a; Vaughan et al., 2003b) and an ex situ approach based on harvesting eggs or nestlings from high risk nests and rearing them in captivity for subsequent release into the wild (Nader et al., 1999).

The fundamental difference between the approaches lies in their perception of the relative importance of quality versus quantity in scarlet macaw production (see Beres and Starfield (2001), Meretsky et al. (2001), and Meretsky et al. (2000) for a similar debate about California condor management). The in situ approach favors quality by producing macaws that are parent-raised, fledge naturally, and are exposed to natural environmental and social stimuli during the post-fledging period. However, potential losses to poaching are high unless nests are protected effectively. The ex situ approach favors quantity by removing eggs or nestlings from high-risk nests to secure captive facilities. In addition to eliminating losses to poaching, potentially more macaws can be produced per breeding pair since females may produce a second clutch after eggs are removed. However, macaws produced ex situ are hand-reared by humans, and their ability to survive and reproduce successfully in the wild upon release is unproven. Reintroductions of captive-reared birds have typically had low success rates (Wiley et al., 1992; Beck et al., 1994; Snyder et al., 1994).

Our findings suggest that the post-fledging period is a sensitive time when young macaws gradually develop the behaviors and social relationships that will determine their success in the wild. We believe this observation underscores the challenges facing ex situ management programs and highlights the importance of natural recruitment where young macaws experience prolonged parental care, experiment with the physical environment at a landscape scale, and gradually adjust to social relationships.

For example in our study, prior to foraging independently macaw fledglings spent several weeks playing with small sticks and leafs as they developed the muscle coordination necessary to handle food items. Similarly, a peak in play among siblings preceded integration with larger groups of macaws outside of the nuclear family. Such opportunities for play during early development are important for enhancing muscular development, promoting learning and experimentation with the environment, and adjusting to social relationships (Ficken, 1977). While these activities may be simulated in captivity through environmental enrichment (Abramson, 1995c), experimental studies of birds suggest that the environmental and social contexts of early learning may influence developmental outcomes (Smith et al., 2002; White et al., 2002). For example, exposure to flocks of mixed age and sex classes early in development may affect mate selection and eventual reproductive success (Freeberg, 2000; Smith et al., 2002).

We also believe that social learning (Fritz and Kotrschal, 1999; Fritz et al., 2000; Midford et al., 2000; Huber et al., 2001; Sherwin et al., 2002) plays a key role in the behavioral development of scarlet macaw fledglings. When the fledglings began to forage independently, their parents led them to *Cordia coloccoca* trees with small, soft fruits easy for young macaws to manipulate and consume. The parents fed on *Cordia* until the fledglings began imitating them, then moved to nearby palms (*Scheelea rostrata*) to feed with other adult macaws. Palm nuts, a preferred food item requiring considerable coordination to harvest and manipulate, were too difficult for fledglings to consume. However, we observed the fledglings follow adults as they hovered and plucked a palm nut from a cluster, perch with them on a nearby branch, and beg as the adult opened and consumed the nut. By week 11, fledglings were clumsily attempting to harvest and open palm nuts themselves. We also believe that inexperienced fledglings learn the locations and seasonal patterns of food resources at a landscape scale by following older, more experienced individuals (Barta and Szep, 1992; Dall Sasha, 2002; Sonerud et al., 2001). Macaws produced ex situ do not experience such learning opportunities in the absence of parental care and exposure to free-ranging wild flocks.

Given these observations, we believe that effective long-term conservation of macaw populations depends upon increasing recruitment of naturally fledged birds through in situ management and protection of nest cavities in cooperation with local communities. While there are examples of captive-raised psittacines (Wiley et al., 1992; Sanz and Grajal, 1998), including macaws (Nycander et al., 1995; Brightsmith, 2000), surviving and successfully reproducing in the wild, in general reintroductions of captive-raised animals have had limited success (Derrickson and Snyder, 1992; Beck et al., 1994; Snyder et al., 1996). Many behavioral deficiencies, including reduced breeding success, unfamiliarity with home ranges, deficient predator avoidance, unnatural dispersal, disrupted social organization, and human imprinting, have been reported in released captive-raised birds (Curio, 1998). We feel that the conservation value of augmenting an existing population not facing immediate extinction is small given the risk of introducing maladaptive behaviors or disease. While hand-reared macaws released in Peru and Costa Rica have demonstrated high short-term survival, released birds may exhibit unnatural behaviors such as not fearing humans or returning frequently to release sites (Nycander et al., 1995; Brightsmith, 2000). Such behaviors are not necessarily detrimental to survival in isolated rainforests but would put macaws at great risk in Central Pacific Costa Rica, with its high human population density.

We do not dismiss the potential of ex situ programs to improve the status of scarlet macaws in Costa Rica; however, such programs should focus on reestablishing populations in parts of their historic range where they have been locally extirpated. Private conservation organizations have initiated such efforts at multiple sites in Costa Rica (Amigos de las Aves, Alajuela, Costa Rica; Zoo Ave, La Garita de Alajuela, Costa Rica). While establishing macaws in areas without resident wild populations may be more difficult than augmenting existing populations for the reasons we have discussed (Wiley et al., 1992), the potential conservation value if successful is great, while risks to existing populations are small.

Our results and future studies of the post-fledging period can aid in developing rearing and release practices that more closely mimic natural development, thereby increasing the probability of successful adaptation of macaws to the wild. We encourage practitioners to give utmost consideration to behavioral issues by developing rearing methods that reduce contact with humans and maximize contact with other macaws, screening release candidates for behavioral deficiencies, and developing soft release techniques that allow young macaws to gradually explore their new ranges in cohesive social groups. We also recommend radiotelemetry as a tool to assess survival and monitor reproduction of released macaws. We found radiotelemetry to be a safe and effective technique, and insufficient monitoring has been a major impediment to assessing the long-term success of avian reintroduction efforts (Earnhardt et al., 2003).

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