

HOW TO KEEP TROPICAL MONTANE FRUGIVOROUS BIRDS IN CAPTIVITY

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Resumen. – Como mantener aves frugívoras de montañas tropicales en cautiverio. – Conforme el estudio de la ornitología Neotropical madura, incrementa el número de investigadores que en lugar de métodos principalmente observacionales de las aves en su entorno natural, utilizan métodos experimentales que a menudo requieren que las aves sean mantenidas en cautiverio. Existen pocos recursos para ayudar al investigador en el diseño de tales estudios en zonas Neotropicales. Aquí presento mi experiencia en el mantenimiento de aves frugívoras silvestres en cautiverio en un bosque húmedo premontano en Costa Rica. Sugiero una serie de protocolos para mejorar la probabilidad de que un ave aprenda rápidamente a comer dieta sintética, y ofrezco sugerencias que pueden aumentar la supervivencia bajo condiciones rústicas en campo. Finalizo con una discusión de factores geográficos, temporales, y específicos que pudieran afectar al éxito de adaptación de un ave a condiciones de cautiverio para guiar la selección de especies en otros estudios.

Abstract. – As the study of Neotropical ornithology matures, increasing numbers of researchers are shifting from primarily observational studies of birds in their natural habitats to experimental studies which often require that birds be kept in captivity. Little guidance currently exists to help researchers plan captive studies of Neotropical species. I report here on experiences bringing wild frugivorous birds into captivity at a premontane forest site in Costa Rica. I suggest protocols that will increase the likelihood that birds will rapidly learn to consume synthetic diet and offer some guidelines that may increase survival probability under rustic field conditions. I conclude by considering geographic, temporal, and species-level factors that may affect the success with which birds adapt to captive conditions to help guide species selection in future studies. *Accepted 31 March 2009.*

Key words: Body condition, captive bird, distress, frugivory, montane forest, synthetic diet, Costa Rica.

INTRODUCTION

The study of Neotropical avifaunas has lagged behind ornithological work in most other regions of the world. As a consequence, the majority of studies published from the Neotropics in recent years still focus on documenting the biodiversity and habitat relations of poorly known avifaunas (e.g., Donegan *et*

al. 2007, Ruiz-Guerra *et al.* 2007, Felton *et al.* 2008), effects of fragmentation and deforestation on that biodiversity (e.g., Restrepo & Gomez 1998, Stratford & Stouffer 1999), reporting on basic natural history, such as movements and reproductive behaviors (e.g., Greeney *et al.* 2006, Capllonch & Ortiz 2007, Karubian *et al.* 2007), or even describing new taxa (e.g., Donegan 2007, Herzog *et al.* 2008). Nevertheless, more and more researchers are building upon this foundation by examining

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questions broadly relevant to the fields of animal behavior (e.g., Beissinger *et al.* 1998, Fusani *et al.* 2007b), life history evolution (e.g., Ferretti *et al.* 2005), and physiological ecology (e.g., Wikelski *et al.* 2000, Fusani *et al.* 2007a) using Neotropical birds. Thus, ornithologists working in Neotropical systems will increasingly be faced with designing new kinds of experimental methods. Many such experiments will involve keeping birds in captivity.

Currently, little information is available to guide the design of captive bird protocols for Neotropical species. Protocols designed for temperate birds are often inappropriate because of species-level differences in diet or physiology (although Neotropical researchers may wish to refer to such publications and adapt them to their system; e.g., Bocetti 1994, Bocetti & Swayne 1995, Asher & Bateson 2008). Often too, Neotropical study sites provide few of the facilities for the care and housing of captive birds typically found at temperate-zone institutions. In the few published studies involving captive Neotropical birds, authors rarely reported their methods in sufficient detail to adequately guide others in designing animal care protocols (e.g., Moermond & Denslow 1983, Levey *et al.* 1984, Wiersma *et al.* 2007, Alves *et al.* 2008). An additional factor that likely contributes to the lack of information is that discussing successful and unsuccessful approaches involves acknowledging that birds sometimes die when protocols fail. Researchers may be reluctant to report mortality if they believe that permission and/or funding for their work would be revoked by such disclosure. Unfortunately, failure to report difficulties (and solutions to such difficulties) means that mistakes are unnecessarily repeated and that protocols are developed through trial and error. As a consequence, birds experience avoidable stress and some die unnecessarily.

I report on experiences keeping a variety of wild frugivorous bird species in captivity at

a remote field site in north-eastern Costa Rica. The primary goals of this study were to examine species-level differences in dietary preference in relation to migratory behavior. The main results of this work will be published elsewhere (Boyle *et al.* in prep.). Here I give a brief description of the site and avifauna, and then comment on protocols that improved the chances that birds would adapt to and remain healthy in captivity. Although my experiences stem from keeping birds in the short-term, many recommendations are applicable to longer-term captive situations.

METHODS

I worked in the Rara Avis reserve at c. 700–800 m a.s.l. on the Atlantic slope of Costa Rica (10°17'3"N, 84°02'47"W). This site is located along an altitudinal gradient of protected forest extending from 30–2900 m elevation. Rara Avis has a mean annual temperature of 23°C and mean (\pm SE) annual rainfall is 8279 mm (\pm 263 mm). Roughly a quarter of the bird species breeding on the Atlantic slope migrate altitudinally (Stiles 1983). Because the main focus of this research was to examine the dietary correlates of migratory behavior, roughly half the birds brought into captivity were altitudinal migrants. I conducted this work during June–July 2002. The months June and July coincide with the end of the breeding season for both residents and migrants and also marks the beginning of downhill migration (Boyle unpubl. data, Stiles & Skutch 1989). I captured birds in understory and canopy mist nets in both old-growth and selectively-logged forest from 06:00 h to 13:00 h or until rain began.

In total, I attempted to keep 54 birds of the following 10 species in captivity (sample sizes in parentheses; names follow the American Ornithologists' Union 1998, 2005):

Pipridae; White-ruffed Manakin (*Corapipo altera*, 16), White-collared Manakin (*Manacus candei*, 6); Tyrannidae; Ochre-bellied Flycatcher (*Mionectes olivaceus*, 9), Olive-striped Flycatcher (*M. oleagineus*, 5); Turdidae; Black-headed Nightingale-Thrush (*Catharus mexicanus*, 4), Black-faced Solitaire (*Myadestes melanops*, 5); Thraupidae; Green Honeycreeper (*Chlorophanes spiza*, 1), Tawny-crested Tanager (*Tachyphonus delatrii*, 2), Silver-throated Tanager (*Tangara icterocephala*, 5), Emerald Tanager (*Tangara florida*, 1). All species are highly frugivorous ($\geq 83\%$ of fecal remains consisting of seeds or indigestible fruit fibers in all species except Black-headed Nightingale-Thrushes from which 64% of fecal remains derived from fruit; Boyle 2006). However, species differed considerably in the identity and relative abundance of fruits in wild diets. I aimed to maintain birds exclusively on a synthetic diet for ≥ 24 h and preferably 2–3 days prior to conducting preference trials. I used Denslow *et al.*'s (1987) banana mash diet for frugivorous birds colored red. I substituted gelatin for agar, as unflavored gelatin was easily and cheaply available in Costa Rican markets, whereas agar was both expensive and difficult to obtain locally. Part way through the field season I experimented with different colorings for the synthetic diet. Based on observations of wild fruit colors, I colored the synthetic diet as black as possible by adding substantial quantities of both red and blue food dye. I additionally offered birds diet colored either orange or blue or both. With each individual, I first offered a selection of different colors until it became apparent which color they preferred.

RESULTS

Getting birds to feed. I followed recommendations in Denslow *et al.* (1987) for encouraging birds to begin foraging in captivity, but apparently had more difficulties than they in induc-

ing birds to switch from natural fruits to the synthetic diet. I initially presented birds with brightly-colored (red) cubes of synthetic diet along with wild-collected fruits known to be present in the diet of each species. At first, I attached whole infructescences to the inside of cages as well as placing loose fruits on top of and around chunks of synthetic diet. Following Denslow *et al.* (1987), I gradually reduced the numbers of wild fruits in hopes that as birds got hungry, they would sample and begin regularly consuming the synthetic diet. However, many birds never consumed much of the synthetic diet. Although virtually every bird tasted at least a small amount of the diet, many would only eat wild fruits, even after several days in captivity. I experimented with altering the concentrations of sugars and fats in the diet but these factors did not affect birds' willingness to feed. Despite monitoring food intake and condition approximately every 2 h between dawn and dusk, four birds died, apparently of starvation. All four individuals died either during their first night in captivity or within a few hours of dawn the following morning. Three of the birds that died were manakins (two White-ruffed Manakins and one White-collared Manakin) and the fourth was an Olive-striped Flycatcher. I dissected one adult male White-ruffed Manakin and was unable to find any subcutaneous body fat. All birds appeared healthy at the time of capture.

Once I began offering birds diet of different colors in addition to red, most began to consume the synthetic diet within hours of capture. The contrast in success rate between black-colored diet and all other colors was striking. Prior to offering the black diet, 48% of the birds either had to be released due to low food intake, or they died as noted above. Following the addition of black coloring, no birds died, and only 22% of birds had to be released due to low intake. Not all species responded to food color in the same way.

Manakins and thrushes would only consume black diet. Tanagers were less selective, but consumed more black diet than diet of other colors. In contrast, *Mionectes* flycatchers preferred red or orange over black. Indeed, if flycatchers are excluded from the dataset, the effect of switching diet color is even more striking; 56% vs 21% (out of 16 and 14 respectively) non-flycatcher individuals had to be released or died prior to vs following coloring diet black.

Both physical and visual presentation of the synthetic diet influenced how quickly a bird would learn to consume the synthetic diet. Species that perch to pluck fruits readily ate diet from petri dishes placed on cage floors. Species that sally to pluck fruits (e.g., manakins) more readily consumed diet when it was offered in small dishes attached to cage walls. *Mionectes* flycatchers consume large quantities of arillate seeds from species in the Clusiaceae. Such seeds are usually presented in 4–10 locules that dehisce in a star-shaped pattern. Flycatchers learned to consume the synthetic diet most rapidly when I filled empty locules of *Clusia* fruits with chunks of diet of a color similar to the arillate seeds (orange or red). Within one day, most flycatchers transitioned from consuming only wild fruit, to diet presented in *Clusia* locules, to diet arranged in a star-shaped pattern mimicking open *Clusia*, to small chunks of diet haphazardly arranged in a dish. This method also was effective with some tanager individuals.

For all species, I found it necessary to provide wild fruits during at least the first day of captivity. I was fortunate to conduct this study during the time of year of maximum fruit production at this site (Boyle 2006). Nevertheless, collecting enough wild fruit for up to eight captive birds involved tremendous researcher effort. Monitoring bird condition and food intake, cleaning cages, and collecting wild fruits for newly-captured birds required

the full-time efforts of at least one field assistant from dawn to dusk, even when caring for as few as four or five birds. I never attempted to keep more than eight birds at a time due to these personnel demands.

Factors associated with transport, housing, and monitoring of newly captured birds. Events occurring during the first 24 h following capture appeared to be the most critical in affecting whether or not an individual bird would adapt to captivity. Thus, researchers should make every attempt to minimize stress and monitor birds as frequently as possible during this period. In the small frugivorous birds I studied, gut passage time was ~30 min. Therefore, I found it necessary to capture birds at locations close enough to housing facilities that the birds could be safely transferred within 30 min. Longer transport times will mean that birds will begin exhausting stored energy reserves even before reaching captive housing. Because trails at Rara Avis are muddy, slippery, and wet, transporting birds by hand in a bird bag was risky due to the danger of the researcher slipping. I found that suspending the bird bags within a durable frame (such as a small wire cage) during transport minimized risk of injury to birds during transport.

Rara Avis, like most Neotropical study sites, lacked designated animal housing facilities. Thus, I was faced with obtaining cages and building or adapting existing structures to accommodate captive birds. I found that purchasing individual cages was straightforward but expensive in pet stores, and that canary breeders were a source for cheaper cages (ask for breeder names at pet stalls in large markets). All the birds in this study needed more perches than those supplied with commercial cages. Additionally, some cages available to us had mesh sizes too large to prevent small birds escaping and larger mesh size would likely have increased the risk of nocturnal predators (e.g., small mammals, snakes) enter-

ing cages. I minimized attracting predators and parasites by lining floors with newspapers (which can be quickly and easily changed while minimizing disturbance to birds) and cleaning cages every several days (and between housing of different individuals) using a dilute bleach solution. I situated cages in a building that was not completely enclosed which had the advantage of ensuring that birds experience natural daylight and temperature regimes but had the drawback of increasing the risk of predators entering the facility. Consequently, I took the precaution of ensuring that cages were securely attached to the base they sat on, and at dusk, wiring closed cage doors, removing all food, and changing cage floor lining.

Once in captivity, I found that birds calmed and began foraging more quickly if they were unable to see any surrounding environs and were not exposed to loud noise. Surrounding each cage with light-weight white cotton cloth secured with clothes pegs during the first few days eliminated the tendency of birds to try to force their way out of cages, and at the same time, allowed natural daylight to illuminate cages. Contrary to Denslow *et al.* (1987), I did not have success placing new birds in the same cages as acclimated birds, although in more social species (e.g., some tanagers) this technique may be effective. Although I did not capture birds past 13:00 h due to afternoon rains at my study site, I found that birds captured later in the morning tended to adapt to captivity more readily than those captured soon after dawn. This was likely due to the fact that birds captured early are still replenishing energy stores depleted over the previous night. Thus, any reduction in food intake may have a greater adverse effect on early than late captures.

Because of the importance of food intake rates to captive health and survival, I found it imperative to monitor intake frequently and establish clear criteria for releasing birds not

responding well to captive conditions. To decide what food intake rate is sufficient to meet the energetic demands of small frugivores, I compared food intake of newly-captured birds to intake rates of birds that adapted well to captive conditions. Intake rates of the frugivorous species I studied were surprisingly high: adult male White-ruffed Manakins would regularly consume their body mass (in whole, fresh fruit including seeds) within ~1.5 h. Larger birds such as Black-faced Solitaires ($31.9 \text{ g} \pm 0.3 \text{ g}$) would generally take > 3 h to consume their body mass.

DISCUSSION

My experiences bringing birds into captivity seemed to differ in important respects from the experiences of other researchers previously working at lower elevations in the same region, despite overlap in bird species between studies. In particular, I had a much shorter window of time in which to induce birds to eat in captivity before their condition began to decline. By the end of my field season, I adopted a 4 h initial captive acclimation period. If an individual did not begin consuming substantial amounts of food (and ideally, begin to eat synthetic diet) within that period, I released it. While this may be conservative for larger birds or individuals with substantial fat stores, it appeared to be appropriate for the birds with the highest metabolic rates at my site. In contrast, researchers at lower elevations had a longer window of 24–48 hours (depending on body mass) to achieve a similar level of acclimation (D. J. Levey pers. com.). Several factors may contribute to the difference in experiences. First, the effect of different temperature (3°C cooler at Rara Avis) and rainfall regimes (roughly double the mean annual rainfall at Rara Avis; 8268 mm vs 4306 mm) could contribute to increased energetic demands for birds living at higher elevations. A related consideration is that birds living in

climatically unpredictable environments may be easier to bring into captivity because they likely can better withstand unexpected reductions in food intake than birds living in more predictable environments. If true, all inner-tropical species may be more challenging to bring into captivity than temperate species. Second, the timing of studies in relation to breeding cycles likely influences fat load and energetic stress. My study was timed to coincide with the end of the breeding season. During breeding, birds invest in displays, territorial activities, egg production, incubation, and feeding of young, frequently at the expense of their own condition. Researchers timing their studies to immediately follow reproduction may thus have greater difficulties getting birds to adapt to captivity due to depleted energy stores and compromised condition relative to researchers studying captive birds at other times of the year.

Because of the apparent importance of food intake to adapting to captivity, I recommend that researchers keep separate logs adjacent to each cage in which they document status reports, quantities of food administered, quantities of food removed from cage, and cleaning events. Signs of well-adapted birds include alertness, preening, frequent (but not obsessive) movements around cage, frequent feeding, and vocal responses to ambient bird sounds. Warning signs include incessant activity, incessant calls, closed eyes, fluffing of body feathers, and listlessness. The last three indicate severe stress and every attempt should be made to induce a bird to eat more early on or to release a bird before they reach this stage. If a bird's condition does decline to critical levels, administering a 15% glucose or fructose solution (not sucrose) via eyedropper to the edge of the bill can resuscitate the individual. The effects of sugar in the bloodstream are apparent almost immediately but they are short-lived. When

deciding where to release birds, researchers should balance the desirability of releasing individuals in familiar territory, with the additional stress imposed by longer transport times.

Small frugivores may be the most challenging among passerines to bring into captivity. Most fruits consumed by small tropical frugivores contain much lower concentrations of sugars than does nectar (mean sugar content of ripe fruits of 15 bird-dispersed species at La Selva Biological Station, Costa Rica: 7.9%; Lumpkin & Boyle in press; typical sugar concentrations in nectar of hummingbird-pollinated flowers: 20–30%; Hainsworth & Wolf 1976, Stiles 1976). Thus, birds primarily consuming fruit must maintain very high intake rates to maintain energy balance. Furthermore, the smaller a bird is, the higher its mass-specific metabolic rate (Calder 1974). Together, this implies that the smaller and the more frugivorous a bird is, the more vigilant the researcher must be to ensure sufficient food intake. Finer-scale dietary attributes may also influence the ease with which researchers can bring birds into captivity. While all species I studied are considered frugivores, all consume some arthropod prey, and clear species-level differences exist in the proportion of arthropods in diets of frugivorous species (Boyle 2006). In the long term, the most highly frugivorous birds may be the easiest to maintain in good condition in captivity (Denslow *et al.* 1987). However, in the short term, the most highly frugivorous birds that rely on a constant intake of simple carbohydrates due to their short, simple digestive tracts (Martínez del Río & Restrepo 1993) may have smaller windows of opportunity to acclimate before going into energetic deficit than more omnivorous species. The smallest and most highly frugivorous birds I studied were White-ruffed Manakins. Mean (\pm SE) mass of adult males in this species is 10.9 g (\pm 0.05 g) and adult females average 12.4 g (\pm 0.08 g).

Fecal samples collected from White-ruffed Manakin males contained an average (\pm SE) of only 2.3% (\pm 0.6%) arthropod remains while the percentage in female samples reached 6.3% (\pm 0.8%). Thus, male White-ruffed Manakins were the most likely of the birds I studied to experience energetic deficits. It is notable that two of the four birds that died were adult male White-ruffed Manakins.

The willingness of birds to consume diet of different colors appeared to be linked to preferences for wild fruits of different colors. All bird species in this study consume a diverse assemblage of wild fruits that are black, blue, red, orange, or white when ripe (Boyle 2006), and fruit color choice seems to differ considerably among individuals within species (Willson & Comet 1993). However, birds do not consume fruits of different colors in equal proportions, nor do they equally prefer fruits of different colors (Boyle 2006). The fruits most prevalent in wild diets of the manakin, thrush, and tanager species in this study are black when ripe, and black is the most prevalent fruit color in at least two Neotropical forests (Wheelwright & Janson 1985). In contrast, the fruits most prevalent in the diets of the flycatchers in this study are red or orange when ripe (Boyle 2006).

The strong effect of color on birds' willingness to consume artificial diet (even after tasting) was a surprise that bears further examination. Birds clearly differ in their visual capabilities (Ödeen & Håstad 2003), and how such variation affects foraging is beginning to be explored (Altschuler 2001, Honkavaara *et al.* 2002, Schaefer *et al.* 2006). If examining foraging in relation to fruit color is not the focus of the study, few researchers will have the means to quantify or control the color of synthetic diet systematically. In such cases, choosing bird species that are relatively unselective with regard to fruit color (in this study, tanagers were the least selective), and offering a variety

of color choices to newly-captured birds will increase the likelihood of success.

A final factor that may influence a birds' energetic status and thus, the time frame that researchers have to acclimate birds, is the mating system and sex of the bird. Many Neotropical frugivorous species, including most species in the Pipridae and Cotingidae, have lek mating systems. In species where lek displays involve acrobatic maneuvers, males may minimize fat stores and body mass to reduce display flight costs and increase agility (Lima 1986, Rogers 1993). All four individuals that died in this study were adult males of lekking species. Researchers thus should avoid sampling adult males of lekking species, or at least to pay special attention to males during initial acclimation.

Neotropical birds provide countless opportunities to address compelling questions in most disciplines of avian biology (Macedo 2008). Continued dominance of the ornithological literature by studies of temperate-zone birds will inevitably lead to erroneous generalizations based on a small fraction of avian biodiversity. Neotropical researchers are encouraged to refer to Gaunt & Oring (1999) for general guidelines for the use of wild birds in scientific research (free download in English, Spanish, or Portuguese from the website of the Ornithological Council at <http://www.nmnh.si.edu/BIRDNET/GuideToUse/>). Additional and more detailed recommendations on captive bird husbandry include Richtie *et al.* (1994; individual chapters available for free download at <http://www.avianmedicine.net/ampa.html>) and King *et al.* (1977). I urge a greater exchange of practical information among Neotropical ornithologists. Such exchanges will benefit birds by improving protocols as well as stimulate more experimental work with Neotropical species which will lead to a broader understanding of avian ecology, behavior, and physiology.

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REFERENCES

- Altshuler, D. L. 2001. Ultraviolet reflectance in fruits, ambient light composition and fruit removal in a tropical forest. *Evol. Ecol. Res.* 3: 767–778.
- Alves, M. A. S., P. D. Ritter, R. D. Antonini, & E. M. Almeida. 2008. Two thrush species as dispersers of *Miconia prasina* (Sw.) DC. (Melastomataceae): an experimental approach. *Braz. J. Biol.* 68: 397–401.
- American Ornithologists' Union. 1998. Checklist of North American Birds, 7th ed. American Ornithologists' Union, Washington, DC.
- American Ornithologists' Union. 2005. Forty-sixth supplement to the American Ornithologists' Union check-list of North American birds. *Auk* 122: 1026–1031.
- Asher, L., & M. Bateson. 2008. Use and husbandry of captive European Starlings (*Sturnus vulgaris*) in scientific research: a review of current practice. *Lab. Anim.* 42: 111–126.
- Beissinger, S. R., S. Tygielski, & B. Elder. 1998. Social constraints on the onset of incubation in a Neotropical parrot: a nestbox addition experiment. *Anim. Behav.* 55: 21–32.
- Bocetti, C. I. 1994. Techniques for prolonged confinement and transport of small insectivorous passerines. *J. Field Ornithol.* 65: 232–236.
- Bocetti, C. I., & D. E. Swayne. 1995. Suggested aviary design and procedures to reduce mortality of captive warblers. *Wildlife Soc. Bull.* 23: 723–725.
- Boyle, W. A. 2006. Why do birds migrate? The role of food, habitat, predation, and competition. Ph.D. diss., Univ. of Arizona, Tucson, Arizona.
- Calder, W. A. 1974. Consequences of body size for avian energetics. Pp. 86–144 in Paynter, R. A. (ed.). *Avian energetics*. Nuttall Ornithol. Club Publ. 15, Cambridge, Massachusetts.
- Capllonch, P., & D. Ortiz. 2007. Does the Masked Yellowthroat (*Geothlypis aequinoctialis velata*) migrate? *Ornitol. Neotrop.* 18: 195–207.
- Denslow, J. S., D. J. Levey, T. C. Moermond, & B. C. Wentworth. 1987. A synthetic diet for fruit-eating birds. *Wilson Bull.* 99: 131–135.
- Donegan, T. M. 2007. A new species of brush finch (Emberizidae: *Atlapetes*) from the northern Central Andes of Colombia. *Bull. Br. Ornithol. Club* 127: 255–268.
- Donegan, T. M., J. E. Avendaño, E. R. Briceño, & B. Huertas. 2007. Range extensions, taxonomic and ecological notes from Serranía de los Yariquies, Colombia's new national park. *Bull. Br. Ornithol. Club* 127: 172–213.
- Felton, A., J. T. Wood, A. M. Felton, B. A. Hennessey, & D. B. Lindenmayer. 2008. A comparison of bird communities in the anthropogenic and natural-tree fall gaps of a reduced-impact logged subtropical forest in Bolivia. *Bird Conserv. Int.* 18: 129–143.
- Ferretti, V., P. E. Llambias, & T. E. Martin. 2005. Life-history variation of a Neotropical thrush challenges food limitation theory. *Proc. R. Soc. Lond. B Biol. Sci.* 272: 769–773.
- Fusani, L., L. B. Day, V. Canoine, D. Reinemann, E. Hernandez, & B. A. Schlinger. 2007a. Androgen and the elaborate courtship behavior of a tropical lekking bird. *Horm. Behav.* 51: 62–68.
- Fusani, L., M. Giordano, L. B. Day, & B. A. Schlinger. 2007b. High-speed video analysis reveals individual variability in the courtship displays of male Golden-collared Manakins. *Ethology* 113: 964–972.
- Gaunt, A. S., & L. W. Oring. 1999. Guidelines to the use of wild birds in research, 2nd ed. The Ornithological Council, Washington, DC.
- Greeney, H. F., R. C. Dobbs, G. I. C. Diaz, S. Kerr, & J. G. Hayhurst. 2006. Breeding biology of the Green-fronted Lancebill (*Doryfera ludovicae*) in eastern Ecuador. *Ornitol. Neotrop.* 17: 321–331.
- Hainsworth, F. R., & L. L. Wolf. 1976. Nectar char-

- acteristics and food selection by hummingbirds. *Oecologia* 25: 101–113.
- Herzog, S. K., M. Kessler, & J. A. Balderrama. 2008. A new species of tyrannulet (Tyrannidae: *Phyllomyias*) from Andean foothills in northwest Bolivia and adjacent Peru. *Auk* 125: 265–276.
- Honkavaara, J., M. Koivula, E. Korpimäki, H. Siitari, & J. Viitala. 2002. Ultraviolet vision and foraging in terrestrial vertebrates. *Oikos* 98: 505–511.
- Karubian, J., L. Carrasco, D. Cabrera, A. Cook, & J. Olivo. 2007. Nesting biology of the Banded Ground-cuckoo (*Neomorphus radiolosus*). *Wilson J. Ornithol.* 119: 221–227.
- King, J. R., T. J. Cade, W. G. Conway, M. R. Fedde, J. P. Hailman, & W. O. Wilson. 1977. Laboratory animal management: wild birds. National Academy of Sciences, Washington, DC.
- Levey, D. J., T. C. Moermond, & J. S. Denslow. 1984. Fruit choice in Neotropical birds: the effects of distance between fruits on preference patterns. *Ecology* 65: 844–850.
- Lima, S. L. 1986. Predation risk and unpredictable feeding conditions: determinants of body mass in birds. *Ecology* 67: 377–385.
- Lumpkin, H. A., & W. A. Boyle in press. Effects of forest age on fruit composition and removal in tropical bird-dispersed understory trees. *J. Trop. Ecol.* 25.
- Macedo, R. H. 2008. Neotropical model systems: social and mating behavior of birds. *Ornitol. Neotrop.* 19: 85–93.
- Martínez del Río, C., & C. Restrepo. 1993. Ecological and behavioral consequences of digestion in frugivorous animals. *Vegetatio* 108: 205–216.
- Moermond, T. C., & J. S. Denslow. 1983. Fruit choice in Neotropical birds: effects of fruit type and accessibility on selectivity. *J. Anim. Ecol.* 52: 407–420.
- Ödeen, A., & O. Håstad. 2003. Complex distribution of avian color vision systems revealed by sequencing the SWS1 opsin from total DNA. *Mol. Biol. Evol.* 20: 855–861.
- Restrepo, C., & N. Gomez. 1998. Responses of understory birds to anthropogenic edges in a Neotropical montane forest. *Ecol. Appl.* 8: 170–183.
- Richtie, B. W., G. J. Harrison, & L. R. Harrison (eds.). 1994. Avian medicine: principles and application. Wingers Publication, Inc., Lakeworth, Florida.
- Rogers, C. M. 1993. Life-history theory in the non-breeding period: trade-offs in avian fat reserves? *Ecology* 74: 419–426.
- Ruiz-Guerra, C., R. Johnston-González, Y. Cifuentes-Sarmiento, F. A. Estela, L. F. Castillo, C. E. Hernández, & L. G. Naranjo. 2007. Noteworthy bird records from the southern Chocó of Colombia. *Bull. Br. Ornithol. Club* 127: 283–293.
- Schaefer, H. M., D. J. Levey, V. Schaefer, & M. L. Avery. 2006. The role of chromatic and achromatic signals for fruit detection by birds. *Behav. Ecol.* 17: 784–789.
- Stiles, F. G. 1976. Taste preferences, color preferences, and flower choice in Hummingbirds. *Condor* 78: 10–26.
- Stiles, F. G. 1983. Birds. Pp. 502–530 in Janzen, D. H. (ed.). *Costa Rican natural history*. Univ. of Chicago Press, Chicago, Illinois.
- Stiles, F. G., & A. F. Skutch. 1989. *A field guide to the birds of Costa Rica*. Cornell Univ. Press, Ithaca, New York.
- Stratford, J. A., & P. C. Stouffer. 1999. Local extinctions of terrestrial insectivorous birds in a fragmented landscape near Manaus, Brazil. *Conserv. Biol.* 13: 1416–1423.
- Wheelwright, N. T., & C. H. Janson. 1985. Colors of fruit displays of bird-dispersed plants in two tropical forests. *Am. Nat.* 126: 777–799.
- Wiersma, P., M. A. Chappell, & J. B. Williams. 2007. Cold- and exercise-induced peak metabolic rates in tropical birds. *Proc. Natl. Acad. Sci. U. S. A.* 104: 20866–20871.
- Wikelski, M., M. Hau, & J. C. Wingfield. 2000. Seasonality of reproduction in a Neotropical rain forest bird. *Ecology* 81: 2458–2472.
- Willson, M. F., & T. A. Comet. 1993. Food choices by Northwestern Crows: experiments with captive, free-ranging and hand-raised birds. *Condor* 95: 596–615.

