



OBSERVATIONS OF NOVEL ADAPTIVE FORAGING STRATEGIES ADOPTED BY PARAGUAYAN BIRDS

PAUL SMITH^{1,2}

¹Fauna Paraguay, Encarnación, Paraguay. www.faunaparaguay.com. E-mail: faunaparaguay@gmail.com.

²Para La Tierra, Reserva Natural Laguna Blanca, Santa Rosa del Aguaray, San Pedro, Paraguay.

Abstract.- Adaptive foraging strategies are beneficial behavioral modifications in response to environmental changes. Observed adaptive foraging strategies are reported for eleven species of Paraguayan birds in the families Falconidae, Rallidae, Caprimulgidae, Cuculidae, Furnariidae and Thraupidae. Spot-winged Falconet *Spizapteryx circumcincta* is suspected to benefit from foraging opportunities created by electricity poles and limited habitat clearance. Slaty-breasted Wood-rail *Aramides saracura* and Black-goggled Tanager *Lanio melanops* are documented exploiting a garbage dump, and the latter is also observed gleaning insects from a building. Examples of adaptive and maladaptive consequences of foraging on insects attracted to lights are detailed in the migrant Scissor-tailed *Hydropsalis torquata* and Little Nightjars *Setopagis parvulus*. Four species of woodcreeper (Furnariidae: Dendrocolaptinae) and Brown Cacholote *Pseudoseisura unirufa* are shown to exploit the same resource (holes in concrete poles) apparently without competing. Hypotheses as to how this might arise are discussed, including the suggestion that bill morphology may cease to be adaptive in this case and actually limit exploitation potential.

Key Words: *Aramides saracura*, *Campylorhamphus trochilirostris*, *Drymornis bridgesii*, *Hydropsalis torquata*, *Lanio melanops*, *Lepidocolaptes angustirostris*, *Pseudoseisura unirufa*, *Setopagis parvula*, *Spizapteryx circumcincta*, *Xiphocolaptes major*

Resumen.- Las estrategias adaptativas de obtención de alimento son modificaciones comportamentales en respuesta a cambios en el ambiente. Se reportan aquí las estrategias adaptativas de obtención de alimento observadas en once especies de aves de Paraguay en las familias Falconidae, Rallidae, Caprimulgidae, Cuculidae, Furnariidae y Thraupidae. El halconcito gris, *Spizapteryx circumcincta*, parece beneficiarse de oportunidades de obtención de alimento generadas por la existencia de postes eléctricos y la limitación del espacio libre. La saracura, *Aramides saracura*, y el frutero corona amarilla, *Lanio melanops*, son reportados sacando provecho de los tiraderos de basura, y en el caso del segundo, también se le observó recogiendo insectos de un edificio. Se detallan ejemplos de consecuencias adaptativas y mal adaptativas de recolección de insectos atraídos a luces en el atajacaminos tijereta, *Hydropsalis torquata*, y en el atajacaminos chico, *Setopagis parvulus*. Se observó que cuatro especies de trepatroncos (Furnariidae: Dendrocolaptinae) así como el caserote castaño, *Pseudoseisura unirufa*, explotan el mismo recurso (agujeros en postes de concreto) aparentemente sin competir entre ellos. Se discuten hipótesis sobre cómo esto pudo haber surgido, incluyendo la sugerencia de que la morfología del pico dejaría de ser adaptativa en este caso, para volverse en realidad un factor limitante en el potencial explotativo.

Palabras claves: *Aramides saracura*, *Campylorhamphus trochilirostris*, *Drymornis bridgesii*, *Hydropsalis torquata*, *Lanio melanops*, *Lepidocolaptes angustirostris*, *Pseudoseisura unirufa*, *Setopagis parvula*, *Spizapteryx circumcincta*, *Xiphocolaptes major*

Adaptive behaviors are positive behavioral reactions to novel situations or environmental changes with a beneficial result to the individual. Though there are exceptions to the rule, standard optimal foraging theory suggests that individuals will favor techniques that provide maximum calorific intake with minimum energetic expenditure (Pyke *et al.*, 1977; Norberg, 1977). However such benefits may need to be

weighed against other factors, including the potential risk to survival (Krebs, 1980; Lucas, 1983; Winterhalder, 1983). Adaptive foraging behaviors may involve minor and possibly unconscious alterations to normal feeding behavior inspired by clumped resources, such as hummingbirds using a feeder (Battistoni *et al.*, 2011); or radical innovative changes of behavior to exploit a rare or novel opportunity, as seen in

tits taking cream from milk bottles in the UK (Fisher & Hinde, 1950).

For many Neotropical bird species very little has been published about foraging strategies beyond brief descriptions of diet and/or typical foraging behavior. In this paper I detail departures from the published foraging strategies for eleven species of Paraguayan birds that were inspired by unusual or changing environmental conditions, and which may thus be considered novel adaptive responses.

RESULTS AND DISCUSSION

Spot-winged Falconet (*Spizapteryx circumcincta*) (Falconidae)

This species has a limited range in Paraguay, being confined to the most arid areas of the Dry Chaco in the extreme west of Departamento Boquerón, most notably in the area in and around Parque Nacional Médanos del Chaco (S20° 07', W61° 00') (Guyra Paraguay, 2005). The relative scarcity of Paraguayan records, all involving isolated observations of single birds, have led to a supposition that the species is rare in the country (Hayes, 1995; Guyra Paraguay, 2004) or at best unobtrusive and difficult to observe. Little published data exists on foraging strategies in this species, but it has been said to "still hunt from cover" (Ferguson-Lees & Christie, 2001), and to feed on "insects (Orthoptera, cicadas), lizards and birds" (Bierregaard, 1994).

An extension of the power lines from PN Teniente Enciso to the Nueva Asunción military base during 2013 saw the installation of concrete posts alongside the Ruta Trans Chaco (in this region a dirt road that sees little traffic) and minor forest clearance. On 29 July 2013 two individuals were observed perched on the newly installed posts, with a typical head-down hunting posture observing the cleared ground around the poles and another individual was observed under similar circumstances on a second visit to the area on 19 September 2013. Similar behavior has also been observed in Argentina where they spend a considerable amount of time sitting on

exposed or semi-exposed perches on trees or posts (M. Pearman, pers. com.).

Though Brown & Amadon (1989) note that "natives" describe the species as a "highly-aggressive ... bird-eater", its rounded wings and slow, flappy flight seem poorly adapted for pursuit hunting. Furthermore Brown & Amadon's (1989) statement that the species "sometimes suns itself on a ... telephone pole", seems incredulous as an explanation at least in its Paraguayan range, where the mean annual temperature is above 25°C (range of monthly means over the period 1951-2011 = 14.2-32.1°C, source Mariscal Estigarribia weather station).

Stomach contents from Argentina, including beetles and caviomorph rodents (M. Pearman pers. com. in Ferguson-Lees & Christie, 2001), are suggestive that at least part of the diet is obtained by dropping to the ground onto prey. However, the habitat where this species is found in Paraguay is characterized by a paucity of large trees, and a dense, low, surrounding thorn forest. Still hunting from cover may thus be a result of the limited availability of suitable hunting perches close to areas of bare ground in this challenging environment. In Argentina Sánchez & Savigny (2005) note that the species is apparently expanding its range into suburban areas and exotic plantations. Consequently if the optimal hunting technique of this species is indeed still-hunting from an exposed perch over open ground, then the installation of these power lines may have created new foraging opportunities for this species, and it could in fact be benefitting from human expansion within its traditional range.

Slaty-breasted Wood Rail (*Aramides saracura*) (Rallidae)

During August 2006 individuals of this Atlantic Forest endemic species were seen regularly sifting through garbage in an open dump within the Atlantic Forest at Hotel Tirol (S27° 11', W55° 46'), Departamento Itapúa. The birds were shy and fled upon noticing the observer, and it was

not possible to determine whether they were feeding on food remains discarded from the hotel or on invertebrates attracted to them.

Little data has been published on foraging habits in this species (Burn, 1996; Taylor & Van Perlo, 1998) but in Provincia Misiones, Argentina, there are reports of the species feeding alongside chickens and other domestic animals (J. Mazar Barnett in litt. in Taylor & Van Perlo, 1998). Though essentially a logical extension of what may be hypothesized to be normal foraging behavior, sifting through garbage is adaptive because it capitalizes upon an unnatural resource within the natural habitat. In other words, the bird is choosing to forage in an unnatural setting despite the availability of typical habitat in close proximity, presumably because of a higher concentration of potential prey.

Little Nightjar (*Setopagis parvula*), Scissor-tailed Nightjar (*Hydropsalis torquata*) (Caprimulgidae)

Feeding on insects attracted to lights is well documented in caprimulgids, and it has been hypothesized that artificial lights may even allow feeding to continue once natural environments nearby have become too dark for hunting to be effective (Holyoak 2001). Both of these species have been observed on several occasions feeding at lights in the Dry Chaco at the headquarters of Parque Nacional Teniente Enciso (S21° 12', W61° 39'), Departamento Boquerón.

Scissor-tailed and Little Nightjars are of seasonal occurrence in the area of the park, the former typically being present in small numbers during the austral winter and the latter being temporarily abundant at least during September/October and February/March when it seems that as yet poorly understood movements are taking place. At least two other species occur in this area, the uncommon winter visitor Band-winged Nightjar (*Systellura longirostris*) and the resident forest-dwelling Rufous Nightjar (*Antrostomus rufus*). Neither of these two species has yet been observed to indulge in similar

behavior. Additional behavioral or ecological factors thus may influence the adoption or otherwise of such behavior.

During the first week of October 2007 a huge aggregation of Little Nightjar numbering many thousands of birds was observed feeding on an emergence of winged termites over the paved Ruta Trans Chaco in the vicinity of the Mennonite Colonies of the Central Chaco (S22° 29', W60° 00'). The insects were attracted to the lights of the passing vehicles and the birds swooped after them repeatedly, resulting in the death of large numbers of individuals through collisions with vehicles.

Maladaptive behavioral changes are detrimental or lethal to the individual. They arise when individuals are unable to accurately assess the costs and benefits of a particular strategy and hence make suboptimal choices (Hollander *et al.*, 2011). Migratory species especially may be time-constrained and must make use of environmental clues that reflect habitat condition, and consequently impact on food availability and fitness (Orians & Wittenberger, 1991; Marshall & Cooper, 2004; Hromada *et al.*, 2008). In this case an abundance of food attracted to vehicle lights represented a lethal maladaptive choice for many individuals but a successful, if high risk, pay off for others.

Brown Cacholote (*Pseudoseisura lophotes*) (Furnariidae), Narrow-billed Woodcreeper (*Lepidocolaptes angustirostris*) (Furnariidae, Dendrocolaptinae), Great Rufous Woodcreeper (*Xiphocolaptes major*) (Furnariidae, Dendrocolaptinae), Scimitar-billed Woodcreeper (*Drymornis bridgesii*) (Furnariidae, Dendrocolaptinae), Red-billed Scythebill (*Campylorhamphus trochilirostris*) (Furnariidae, Dendrocolaptinae)

Individuals of all these species habitually and methodically search bored holes on concrete posts holding up power lines at PN Teniente Enciso, Departamento Boquerón (S21° 12', W61°

39'). The 9 m high rectangular posts were first installed in late 2004 (M. Torales pers. com.) and the upper end of the post each contains 14 round holes of 20 mm diameter on each face that are bored through to the other side. Searching of these holes by these species has been observed there regularly, particularly during the first hours of daylight, since the author's first visit in July 2006. Though it may be viewed to some degree as an extension of the typical foraging methods employed by these species on vertical services, the wide variety of strategies employed by these species in a natural setting is reflected in the great diversity of bill form that they exhibit (Marantz *et al.*, 2003). Probing already bored holes thus involves an adaptive divergence from the typical evolutionary uses of these differing bill forms in some cases.

The exploitation of this single resource by multiple related species raises interesting research questions. Interspecific observational learning and cultural transmission about the location and nature of potential feeding places may have occurred (Krebs, 1973; Vickery *et al.*, 1981) or alternatively the resource may have been discovered accidentally and independently by each of the species through their habit of perching on vertical surfaces.

Chapman & Rosenberg (1991) noted considerable dietary overlap in some Amazonian woodcreepers, and that resources were partitioned in relation to substrate use and foraging height. Puebla-Olivares (2001) also found that dietary overlap occurred in Mexico, but that resources were partitioned according to prey size rather than prey type. Pierpont (1986) positively correlated overlap in diet and substrate use in Peruvian woodcreepers with interspecific territoriality and aggression, demonstrating that those species in direct competition were the most likely to exclude each other aggressively. A lack of observed aggression in this case may thus be hypothesized to reflect a lack of competition among the species.

Bill morphology and variations in feeding

ecology may not only affect diet (Torok, 1990; Chapman & Rosenberg, 1991; Gurd, 2007), but can also result in a differing capacity for the exploitation of a fixed resource. In this case, woodcreepers are probing holes in concrete poles which they are not able to modify through employment of their typical feeding techniques. Depth of probing is restricted by bill length, extent of aperture of the mandibles is related to thickness of the bill and the angle of the probe is determined by bill curvature. Consequently the ability to exploit this resource is limited and not enhanced by their bill morphology. Coupled with possible partitioning in relation to prey size as suggested by Puebla-Olivares (2001) this potentially could partition the resources in a manner largely unrelated to behavior, thereby enabling successful and continual exploitation by a variety of species (Marantz *et al.*, 2003).

Black-goggled Tanagers (*Lanio melanops*) (Thraupidae), Narrow-billed Woodcreeper (*Lepidocolaptes angustirostris*) (Furnariidae), Dendrocolaptinae)

Black-goggled Tanager is omnivorous, but primarily insectivorous, with army ant following and sallying for insects already documented in their normal foraging behaviour (Isler & Isler, 1999). Two variations on this foraging style were observed at Hotel Tirol (S27° 11', W55° 46'), Departamento Itapúa.

During August 2006 several individuals were observed sallying for insects over an open garbage dump with the forest. The birds sallied in short flights (c 3-4 m) from a low perch approximately 30 cm above the ground at the edge of the dump, snapping at insects attracted to the garbage. One male also hovered briefly over the garbage at a height of approximately 40 cm and plunged into grass growing amongst it before returning to its perch with an insect. This is an adaptive behavior presumably inspired by a concentration of insect prey, but does not involve a radical diversion from normal foraging behavior.

At sunrise on 15 September 2007 a small

flock were observed perched on a low wall, periodically flying up to glean moths from the partially mirrored windows of the events hall. The behavior continued for approximately ten minutes before the birds retreated into the forest. Though clearly related to normal gleaning behavior, the fact that the birds had emerged from the forest to exploit the insects that had been attracted to lights during the previous evening suggests a considerable degree of adaptation, requiring a departure from both the normal habitat preference (forest interior) and the ability to over-ride the usual caution associated with the proximity of humans. This suggests that the nutritional pay offs from such behavior were correspondingly high enough to offset the risks (Krebs, 1980). Similar behavior was also observed at first light on two consecutive mornings (12 and 13 October 2013) by a Narrow-billed Woodcreeper *Lepidocolaptes angustirostris*, gleaning insects attracted to lights from under a roof at the accommodation building at Fortín Toledo, Departamento Boquerón (S22° 19', W60° 21')

CONCLUSIONS

These observations demonstrate that foraging strategies in birds are not fixed and in some cases may be highly adaptable in response to changing local conditions. The published literature is guilty in some instances of over-generalizing foraging behavior and diet, and thus fails to properly emphasize the plasticity of such approaches. Such knowledge of adaptability is important when identifying potential threats to species resulting from habitat modification, and also in prioritizing conservation actions effectively. The full extent of foraging behaviors in most Neotropical birds remains underestimated; more detailed studies on individual and community foraging strategies are urgently required to fill the existing gaps in our knowledge.

ACKNOWLEDGEMENTS

Many thanks to Mark Pearman for his useful

comments on certain parts of the manuscript. Thanks also to the people, too numerous to mention individually, who have accompanied me in the field over the years when these observations were made. The hospitality of Mario Torales at Parque Nacional Tte Enciso and Juan Campos at Toledo is greatly appreciated during our frequent visits to the Chaco.

LITERATURE

- Battistoni, M., E. Beck, S. Remsen & F. Wang. 2011. Energy optimization and foraging preference in hummingbirds. *Dartmouth Undergraduate Journal of Science*, Spring: 34-36.
- Bierregard, R. O. 1994. *Spizapteryx circumcinctus*. Pp 254-255 In: del Hoyo, J., A. Elliott, & J. Sargatal (eds). *Handbook of the Birds of the World Volume 2 New World Vultures to Guinea-fowls*. Lynx Edicions, Barcelona, Spain.
- Burn, H. 1996. Genus *Aramides*. Pp. 175-177 In: del Hoyo, J., A. Elliott, & J. Sargatal (eds). *Handbook of the Birds of the World. Volume 3. Hoatzin to Auks*. Lynx Edicions, Barcelona, Spain.
- Brown, L. & D. Amadon. 1989. *Eagles, Hawks and Falcons of the World*. Wellfleet Press, New Jersey, USA, 945 pp.
- Chapman, A. & K. V. Rosenberg. 1991. Diets of four sympatric Amazonian woodcreepers (Dendrocolaptidae). *Condor*, 93: 904-915.
- Fisher, J. & R. A. Hinde. 1950. The opening of milk bottles by birds. *British Birds*, 42: 347-357.
- Gurd, D. B. 2007. Predicting resource partitioning and community organization of filter-feeding dabbling ducks from functional morphology. *American Naturalist*, 169: 334-343.
- Guyra Paraguay. 2004. *Lista Comentada de las Aves del Paraguay*. Guyra Paraguay, Asunción, Paraguay, 200 pp.
- Guyra Paraguay. 2005. *Atlas de las Aves de*

- Paraguay. Guyra Paraguay, Asunción, Paraguay, 212 pp.
- Hayes, F. E. 1995. Status, distribution and biogeography of the birds of Paraguay. American Birding Association Monographs in Field Ornithology, 1: 1–230.
- Hollander, F. A., H. Van Dyck, G. San Martín & N. Titeux. 2011. Maladaptive habitat selection of a migratory passerine bird in a human-modified landscape. *Plos One*, 6(9): 1-11.
- Holyoak, D. T. 2001. Nightjars and their Allies. Oxford University Press, Oxford, UK. 848 pp.
- Gill, F. & D. Donsker (eds). 2010. IOC world bird names (version 3.4). Available at <http://www.worldbirdnames.org/> [Accessed "5 September 2013"].
- Hromada, M., M. Antczak, T. J. Valone & P. Tryjanowski. 2008. Settling decisions and heterospecific social information use in shrikes. *Plos One*, 3(12): 1-5.
- Isler, M. L. & P. R. Isler. 1999. Helm Identification Guides: Tanagers. Christopher Helm, London, UK. 406 pp.
- Krebs, J. R. 1973. Social learning and significance of mixed-species flocks of chickadees (*Parus* spp.). *Canadian Journal of Zoology*, 51: 1275-1288.
- Krebs, J. R. 1980. Optimal foraging, predation risk and territory defence. *Ardea*, 68: 83-90
- Lucas, J. R. 1983. The role of foraging time constraints and variable prey encounter in optimal diet choice. *American Naturalist*, 122: 191-209.
- Marantz, C.A., A. Aleixo, L. R. Bevier, & M. A. Patten. 2003. Dendrocolaptidae. Pp 358-447. In: del Hoyo, J., A. Elliott, & D. Christie (eds). Handbook of the Birds of the World Volume 8 Broadbills to Tapaculos. Lynx Edicions, Barcelona, Spain.
- Marshall, M. R., & R. J. Cooper. 2004. Territory size of a migratory songbird in response to caterpillar density and foliage structure. *Ecology*, 85: 432-445.
- Norberg, R. A. 1977. An ecological theory on foraging time and energetics and choice of optimal food-searching method. *Journal of Animal Ecology*, 46: 511–529.
- Orians, G. H. & J. F. Wittenberger. 1991. Spatial and temporal scales in habitat selection. *American Naturalist*, 137: 29-49.
- Payne, R. B. 2005. The Cuckoos. Oxford University Press, Oxford, UK, 644 pp.
- Pierpont, J. 1986. Interspecific aggression and the ecology of woodcreepers (Aves: Dendrocolaptidae). PhD. diss., Princeton University, New York, USA. [Not seen by author.]
- Puebla-Olivares, F. 2001. Aspectos ecológicos de la familia Dendrocolaptidae (Aves) en la localidad de Yaxchilán, Chiapas, México. Tesis de maestría, Universidad Nacional Autónoma de México, México DF.
- Pyke, G. H., H. R. Pulliam & E. L. Charnov. 1977. Optimal foraging: a selective review of theory and tests. *Quarterly Review of Biology*, 52: 137-154.
- Sánchez, K. B. & C. Savigny. 2005. Nuevos registros del halconcito gris (*Spiziatpteryx circumcinctus*) en el sudeste de la Provincia de Buenos Aires, Argentina. *Nuestras Aves*, 49: 35-36.
- Taylor, B. & B. Van Perlo. 1998. Rails. A Guide to the Rails, Crakes, Gallinules and Coots of the World. Pica Press, Surrey, UK, 600 pp.
- Torok, J. 1990. Resource partitioning among three woodpecker species *Dendrocopos* spp. during the breeding season. *Holarctic Ecology*, 13: 257-264.
- Vickery, W. L., L. A. Giraldeau, J. J. Templeton, D. L. Kramer & C. A. Chapman. 1981. Producers, scrounging and group foraging. *American Naturalist*, 137: 847-863.
- Winterhalder, B. 1983. Opportunity-cost foraging models for stationary and mobile predators. *American Naturalist*, 122: 73-84.