WILLSON, M. F., S. M. GENDE, AND B. H. MARSTON. 1998. Fishes and the forest. BioScience 48:455–462.
WILLSON, M. F., AND K. C. HALUPKA. 1995. Anadromous fish as keystone species in vertebrate communities. Conservation Biology 9:489–497.
WILLSON, M. F., S. M. GENDE, AND P. A. BISSON. In press. Anadromous fishes as ecological links between ocean, fresh water, and land. *In* G. Polis, M. Power, and G. Huxel [EDS.], Foodwebs at the landscape level. University of Chicago Press, Chicago, IL.
WIPFLI, M. S., J. HUDSON, AND J. CAOUETTE. 1998. Influence of salmon carcasses on stream productivity: response of biofilm and benthic macroinvertebrates in southeastern Alaska, U.S.A. Canadian Journal of Fisheries and Aquatic Science 55: 1503–1511.
WIPFLI, M. S., J. P. HUDSON, D. T. CHALONER, AND J. P. CAOUETTE. 1999. Influence of salmon spawner densities on stream productivity in southeast Alaska. Canadian Journal of Fisheries and Aquatic Science 56:1600–1611.

The Condor 103:629–633

BIVOUAC CHECKING, A NOVEL BEHAVIOR DISTINGUISHING OBLIGATE FROM OPPORTUNISTIC SPECIES OF ARMY-ANT-FOLLOWING BIRDS

MONICA BETH SWARTZ[1]
Integrative Biology, School of Biological Sciences, The University of Texas at Austin, Austin, TX 78712

Abstract. As swarms of the army ant *Eciton burchelli* forage across forest floors of the lowland Neotropics, birds gather to eat arthropods flushed by the advancing ants. Past efforts to distinguish members of the obligate ant-following bird guild from the many species that forage opportunistically with army ants have been inadequate. Obligate ant-followers track the locations of multiple nomadic ant colonies in order to maintain a consistent food supply. Each morning, they visit the bivouac site of each colony they are monitoring to assess the ants' activity. Only species dependent upon foraging with army ants exhibit this specialized bivouac checking behavior. This paper proposes a new method for distinguishing between obligate and opportunistic ant-following birds by observing which species check bivouacs.

Key words: *antbird, ant-following birds, army ants, Costa Rica,* Eciton burchelli*, woodcreeper.*

Verificación de Vivaques, un Comportamiento Nuevo que Distingue a Especies Obligatorias de Especies Oportunistas Rastreadores de Hormigas-Ejército

Resumen. Cuando enjambres de la hormiga ejército *Eciton burchelli* forrajean en los suelos de los bosques bajos Neotropicales, algunas aves se aglomeran para ingerir artrópodos espantados por las hormigas que avanzan. Esfuerzos pasados para distinguir entre aquellos miembros del gremio de aves que rastrean las hormigas obligatoriamente de las muchas especies que forrajean de manera oportunista con hormigas ejército han sido inadecuados. Seguidores obligatorios de las hormigas rastrean los sitios de varias colonias nómadas de hormigas a fin de mantener un suministro consistente de alimentos. Cada mañana, estas aves visitan el sitio de vivaque de cada una de las colonias que controlan con fin de evaluar las actividades de las hormigas. Sólo aquellas especies que dependen del forrajeo de las hormigas ejército manifiestan este comportamiento especializado de verificar los vivaques. Este artículo propone un nuevo método para distinguir entre las aves oportunistas y las aves obligatorias rastreadoras de hormigas mediante la observación de aquellas especies que verifican los vivaques.

Many species of tropical birds forage on arthropods escaping from swarm-raiding army ants (Willis and Oniki 1978). Most of these species are opportunists, taking advantage of the plentiful food made available when ants forage through their territory. A few species, mainly in the families Thamnophilidae and Dendrocolaptidae, depend on army ants to flush the majority of their food and are most often found with army ants. Distinguishing between species that forage with army ants regularly but opportunistically and species that depend on following army ants as their primary food source is necessary in order to define the ant-following guild and provide a basis for understanding their shared ecology. I propose a new method for distinguishing between obligate and opportunistic ant-fol-

Manuscript received 2 March 2000; accepted 17 April 2001.
[1] E-mail: mswartz@mail.utexas.edu

lowers based on bivouac checking, an easily observed behavior shared by obligate species that indicates their dependence on army ants.

Previous researchers have sought to categorize dependent species separately from opportunistic species, but vary widely on the criteria and terminology used (Willis and Oniki 1978 and citations therein, Karr 1982, Chesser 1995, Mason 1996). The proposed definition had been that ''professional'' ant-followers obtain more than 50% of their food at army ant swarms (Oniki 1972, Oniki and Willis 1972); however, this measure has never been applied. Harper (1987) was the first to create a methodology to classify ant-followers. Mist-netting in Manaus, Brazil, he found that four species were captured significantly more often in the presence of raiding army ants than in their absence. He called these species ''primary'' ant-followers, while other species that foraged with army ants were ''secondary'' ant-followers. However, this technique is ineffective for classifying species that are rarely caught in mist nets and may incorrectly classify species that change their behavior while foraging with ants, thus altering their capture probability. It also does not directly address the level of dependence necessary to distinguish members of the ant-following guild.

Two Neotropical species of army ants attract birds regularly, *Eciton burchelli* and *Labidus praedator*. Colonies of swarm-raiding army ants are rare enough to make chance encounters with foraging ants an unreliable food source for birds. A colony typically forages over new ground each day (Swartz 1997), so a bird returning to a previous foraging site will seldom relocate the ants. Army ant colonies are nomadic and usually move their bivouacs (huge temporary nests constructed of the ants′ living bodies) at night. By locating and tracking an army ant bivouac, a bird can obtain constant access to foraging army ants by following the connecting trail from the bivouac to the foraging front. Birds can reliably relocate only *E. burchelli* colonies, because *L. praedator* bivouac below ground and resurface to forage only unpredictably. *E. burchelli* bivouacs are typically found under fallen logs or at bases of trees, although during the statary period (a 20-day period of the reproductive cycle in which the colony returns to the same bivouac each day), bivouacs are less readily visible than during the nomadic period (in this study, 5 of 40 statary bivouacs were not readily visible to a human observer). Although a potentially rich food-flushing resource, *E. burchelli* colonies neither forage regularly (on only 65–75% of days in the statary period), nor remain in a constant location (<3 days at any site in the 14-day nomadic period; Swartz 1997).

An obligate ant-following bird species, therefore, cannot depend on only one colony, but must memorize locations and track multiple colonies in space and time. To accomplish this task, ant-following obligates have developed an elaborate suite of behaviors. One behavior practiced by all obligates is bivouac checking, a close examination of the bivouac by the bird to determine if the ants are actively foraging, are present but not foraging (inactive), or have departed the bivouac site. Whether or not an ant-following species practices this specialized tactic may be a simple index of their specialization and an improved criterion to distinguish obligates from opportunists.

METHODS

Between July 1990 and March 1994, I located and tracked *Eciton burchelli* colonies within a 54.7-ha primary lowland rainforest study site near the Sirena Biological Station in Costa Rica's Parque Nacional Corcovado (8°29′N, 83°36′W). I color-banded the army-ant-following birds associated with the colonies in the study site and observed them at ant swarms and at colony bivouac sites. Color-band identification allowed accurate counts of the numbers of individuals and species foraging at 238 *E. burchelli* swarms. Most birds were habituated to foraging in the presence of the observer, and foraged without disturbance or interruption while data were taken.

From inconspicuous positions 5–15 m from inactive bivouacs, I conducted 15 ''bivouac vigils'' to document bivouac checking behavior. Vigils began when morning light was sufficient for accurate viewing and ended when ant foraging activity began (mean vigil duration = 3 hr, 4 min; 46 hr, 5 min total). All birds observed on the five trees nearest the bivouac, on the ground beside the bivouac, or on the log containing the bivouac, and observed to look directly at the bivouac or closely examine the bivouac site were considered to be checking the bivouac. A bivouac check was defined as the arrival of a bird or bird group (pair or family) to the observed area until departure from the observed area, with conspicuous bivouac checking occurring during that interval. Occasionally, a bird or bird group would move away from the bivouac or circle the site before returning. In these cases, only the initial visit of a bird or bird group was recorded as a check. In addition to during vigils, bivouac checks were recorded when birds were observed at bivouac sites with ants retreating from foraging, at inactive bivouacs, or at sites vacated by ants the previous night. Values reported are means ± SD.

RESULTS

I noted 199 bivouac checks at inactive, retreating, or vacated bivouac sites. Seven species of birds checked inactive bivouacs in 142 checking events (Table 1). The four species that checked bivouacs most frequently (Table 1) were also the same four species most frequently found foraging on arthropods flushed by *E. burchelli* (Table 1). The remaining three species seen checking bivouacs were seen on only a few occasions (Table 1).

During the 15 bivouac vigils, 222 birds checked the bivouacs on 134 occasions with means of 4 checks per hour and 6 birds per hour (1.7 ± 0.4 birds per checking event). When possible I timed how long each bird or group of birds spent checking the bivouac (*Dendrocincla anabatina*: 94 ± 96 sec, n = 12; *Gymnopithys leucaspis*: 357 ± 267 sec, n = 19; *Eucometis penicillata*: 150 ± 146 sec, n = 35; *Dendrocolaptes sanctithomae*: 150 ± 173 sec, n = 9; the latter three species each had one to two outliers not included). It was often difficult to read band combinations during such short periods while remaining inconspicuous, but in 13 cases (*D. anabatina*: 3 cases, *G. leucaspis*: 8, *D. sanctitho-*

TABLE 1. Frequency of occurrence (%) and mean (± SD) number of individuals at swarms (n = 238 swarms) for the 15 species most frequently seen foraging at *Eciton burchelli* swarms in Corcovado National Park, Costa Rica, and the number of birds observed checking inactive bivouacs (n = 36) in 142 checking events (defined as a bird or group of birds of one species perching next to and looking at an *Eciton burchelli* bivouac).

		Frequency of occurrence at swarms	Mean number of individuals at swarms	Number of birds checking inactive bivouacs
Tawny-winged Woodcreeper[a,b]	*Dendrocincla anabatina*	84	2.2 ± 1.2	36
Bicolored Antbird[a,b]	*Gymnopithys leucaspis*	82	4.0 ± 2.0	69
Gray-headed Tanager[a,b]	*Eucometis penicillata*	82	3.1 ± 1.5	158
Northern Barred Woodcreeper[a,b]	*Dendrocolaptes sancitithomae*	52	1.6 ± 0.8	13
Chestnut-backed Antbird	*Myrmeciza exsul*	48	1.8 ± 0.6	
Black-faced Antthrush	*Formicarius analis*	22	1.2 ± 0.5	3
Black-cheeked Ant-Tanager[a]	*Habia atrimaxillaris*	21	2.0 ± 0.6	3
Cocoa Woodcreeper	*Xiphorhynchus susurrans*	21	1.1 ± 0.4	2
White-whiskered Puffbird	*Malacoptila panamensis*	21	1.3 ± 0.5	
Black-hooded Antshrike	*Thamnophilus bridgesi*	10	1.4 ± 0.5	
Blue-crowned Manakin	*Pipra coronata*	9	1.3 ± 0.9	
Riverside Wren	*Thryothorus semibadius*	8	1.2 ± 0.4	
Orange-billed Sparrow	*Arremon aurantiirostris*	8	1.1 ± 0.3	
Ochre-bellied flycatcher	*Mionectes oleagineus*	7	1.1 ± 0.2	
Red-capped Manakin	*Pipra mentalis*	7	1.2 ± 0.4	

[a] Also observed checking bivouac sites vacated the previous night.
[b] Also observed checking bivouac sites at the end of the day after the ants had stopped foraging.

mae: 2), the mean return interval for individual birds was about one hour (72.6 ± 47.6 min).

DISCUSSION

Bivouac checking identifies which species of ant-followers are dependent on army ants and may indicate their level of dependence. The four species that checked bivouacs most frequently were also the same four species most frequently found foraging with *Eciton burchelli.* The relative frequency of bivouac checking by these four species reflects their relative population densities (Willis 1974, Karr 1982, Brawn et al. 1995, Swartz, unpubl. data).

The comparatively rare checks of three other species may be the result of several factors. Though these three species (or individuals within these species) depend on the ant swarms for much of their food and have developed the bivouac checking behavior, they are also seen foraging away from ants, and their relative infrequency of checking may reflect their greater independence. Also, there may be individual variance in expression, or life-history-dependent expression, of this behavioral trait within a population. For example, Willis (1992) observed in Manaus that juveniles of *Dendrocolaptes certhia* were more likely to follow army ants than adults. Observer bias may influence results with *Formicarius analis* and *Habia atrimaxillaris,* which are very shy and may not approach even a well-hidden observer at a bivouac. Additionally, territoriality or microhabitat restrictions to species distributions may lower overall bivouac checking frequencies if bivouacs happen to be located outside the territory or preferred microhabitat of individuals (*Habia atrimaxillaris* distributions appeared to be restricted to specific stream drainages; Swartz, unpubl. data). A lower frequency of bivouac checking may also simply indicate the relative rarity of a species. Further research is needed to resolve whether these species are equally dependent on army ants or if another category of dependency is necessary.

Drawing from my observations, I propose the following scenario. Each morning, obligate species visit bivouacs they are tracking. Flying directly into the bivouac location, the birds land on the nearest perch, sometimes only inches from the ants, and look at the bivouac and the ground around it. If the ants are foraging, the birds follow the trail of ants to the swarm. If the ants are inactive, they fly on to the next bivouac along their morning circuit. The number of bivouacs a bird monitors is unknown, although a minimum of three bivouacs is probable to maintain a constant source of food. I observed banded individuals of three species, *Dendrocincla anabatina, Gymnopithys leucaspis,* and *Eucometis penicillata,* foraging with three different ant colonies in three days; on 22 occasions, banded individuals were observed foraging with two different ant colonies on the same day (11, 8, and 3 times for each species, respectively). Tracking obligate ant-followers using radio-telemetry techniques is needed to determine how far these birds travel each day and how many bivouacs they track.

Checking bivouacs sequentially until they encounter a bivouac with a foraging column reinforces the birds' spatial knowledge of multiple bivouac locations and each bivouac's status. When a swarm they are foraging with stops for the day, some species follow the trail of ants back to the bivouac to examine it, then fly on to the next bivouac in their circuit, or to their roost site if the day is over. This may reinforce spatial memory of the bivouac location and of the foraging path taken in case the bivouac moves that night. If a bivouac appears to be gone, they will carefully examine the site to see if the bivouac has shifted position and become less visible. If they cannot find it, they will search for it along the path of the previous day's raid. Occasionally, nomadic ant groups are difficult to relocate and searching birds will fly back to the former bivouac site repeatedly, perhaps for spatial orientation. Obligate ant-followers are exceptionally long lived (Karr et al. 1990, Brawn et al. 1995) and have extended periods of parental care (Swartz, unpubl. data), perhaps to learn, while traveling with their parents, the elaborate behaviors necessary to spatially and temporally track multiple bivouac locations.

Numerous lists have been published of species observed foraging with army ants (Willis and Oniki 1992 and citations therein). Foraging army ants create such a rich food source that almost all insectivorous species inhabiting the forest understory are seen at a swarm eventually. It is tempting to use lists or observations of frequency of foraging with army ants as a measure of dependency. However, very common opportunistic species can occur more frequently than rare ant-following obligates. For example, *Myrmeciza exsul*, with attendance at nearly fifty percent of swarms (Table 1), is a common understory species that forages opportunistically with ants whenever a swarm passes through its small territory. Pairs and family groups of *M. exsul* neither check bivouacs nor forage all day with ants, as they are replaced by conspecifics when the swarm enters a neighbor's territory. Lists of species observed foraging with army ants are best used to compare behavioral differences within a species over a large portion of its range, as populations of some species (e.g., *Eucometis penicillata* and *Formicarius analis*) differ greatly in their reliance on army ants (Willis 1985, Robinson and Terborgh 1995). Also, lists of species observed foraging at swarms may miss important relationships if dependent species are shy (i.e., *Neomorphus* ground-cuckoos) or forage away from the main swarm (for example, *Formicarius analis* often foraged from army-ant return trails at Corcovado, and I believe it to be a kleptoparasite of army ant prey at that site).

Bivouac checking is both time and energy intensive; therefore, it is likely that only obligate species (birds dependent on foraging with army ants) will practice it. Even very rare army-ant-following obligate species can be detected by observing bivouac checking (e.g., I observed *Neomorphus* checking bivouacs in Peru, unpubl. data), as birds need to monitor more bivouacs than they will forage with in a day in order to ensure food availability every day. Establishing bivouac vigils two to three times at one or more bivouacs in the early or late statary phase will likely reveal the complete obligate ant-following bird community, including rare and wary species such as *Neomorphus*. Species observed foraging at swarms, but not checking bivouacs, can be labeled opportunists, since they are not relocating swarms reliably nor monitoring additional ''backup'' colonies for when a colony fails to forage or moves away.

Bivouac checking behavior is a conspicuous display of ant-following birds' ability to track the location of known bivouacs. These birds fly (or walk) directly to the spot nearest the ants, look at the bivouac intently, and then, presumably, fly to the next colony on their circuit. Since these birds are easily disturbed and the duration of the event is short, the importance of this behavior may not have been recognized in the past. By observing whether birds exhibit bivouac checking behavior, we can index their level of specialization on army ants and determine the membership of the obligate ant-following guild at any given location.

Eternal thanks to my indefatigable assistants, D. Hutchinson and D. Coleman. Invaluable help and advice toward the writing of this paper was provided by D. Hutchinson, P. Stouffer, Federico Prado, W. Hodges, L. Ramakrishnan, the *Condor* editors, and two anonymous reviewers. This research was generously supported by the following: David Bruton, Jr. Fellowship, Ari Yehiel Blattstein Endowed Presidential Scholarship, University of Texas Department of Zoology Research Fellowship, Fulbright Fellowship (Institute of International Education), The Explorers Club of New York Exploration Grant, Institute of Latin American Studies Faculty-Sponsored Dissertation Grant, Sigma Xi Grants-in-Aid of Graduate Research, Percy Sladen Memorial Fund Grant (The Linnean Society of London), and L. I. Stengl Graduate Research Fellowships. Special thanks to the Servicio de Parques Nacionales de Costa Rica and the staff of Parque Nacional Corcovado.

LITERATURE CITED

BRAWN, J. D., J. R. KARR, AND J. D. NICHOLS. 1995. Demography of birds in a Neotropical forest: effects of allometry, taxonomy, and ecology. Ecology 76:41–51

CHESSER, T. R. 1995. Comparative diets of obligate ant-following birds at a site in northern Bolivia. Biotropica 27:382–390.

HARPER, L. H. 1987. The conservation of ant-following birds in central Amazonian forest fragments. Ph.D. dissertation, State University of New York, Albany, NY.

KARR, J. R. 1982. Population variability and extinction in the avifauna of a tropical land bridge island. Ecology 63:1975–1978.

KARR, J. R., J. D. NICHOLS, M. K. KLIMKIEWICZ, AND J. D. BRAWN. 1990. Survival rates of birds of tropical and temperate forests: will the dogma survive? American Naturalist 136:277–291.

MASON, D. 1996. Responses of Venezuelan understory birds to selective logging, enrichment strips, and vine cutting. Biotropica 28:296–309.

ONIKI, Y. 1972. Studies of the guild of ant-following birds at Belem, Brazil. Acta Amazonica 2:59–79.

ONIKI, Y., AND E. O. WILLIS. 1972. Studies of the guild of ant-following birds north of the eastern Amazon. Acta Amazonica 2:127–151.

ROBINSON, S. K., AND J. TERBORGH. 1995. Interspecific aggression and habitat selection by Amazonian birds. Journal of Animal Ecology 64:1–11.

SWARTZ, M. B. 1997. Behavioral and population ecology of the army ant *Eciton burchelli* and ant-following birds. Ph.D. dissertation, University of Texas, Austin, TX.

WILLIS, E. O. 1974. Populations and local extinctions of birds on Barro Colorado Island, Panama. Ecological Monographs 44:153–169.

WILLIS, E. O. 1985. Behavior and systematic status of gray-headed tanagers (*Trichothraupis penicillata*, Emberizidae). Naturalia 10:113–145.

WILLIS, E. O. 1992. Comportamento e ecologia do arapaçu-barrado *Dendrocolaptes certhia* (Aves, Dendrocolaptidae). Boletim do Museu Paraense Emílio Goeldi, série Zoologia 8:151–215.

WILLIS, E. O., AND Y. ONIKI. 1978. Birds and army ants. Annual Review of Ecology and Systematics 9:243–263.

WILLIS, E. O., AND Y. ONIKI. 1992. As aves e as formigas de correição. Boletim do Museu Paraense Emílio Goeldi, série Zoologia 8:123–215.

The Condor 103:633–638

FORAGING BEFORE SPRING MIGRATION AND BEFORE BREEDING IN COMMON EIDERS: DOES HYPERPHAGIA OCCUR?

MAGELLA GUILLEMETTE[1]
Département de Biologie et des Sciences de la Santé, Université du Québec à Rimouski, 300 Allée des Ursulines, Rimouski, Québec G5L 3A1, Canada

Abstract. Foraging performance of Common Eider (*Somateria mollissima*) was studied to find out if hyperphagia occurs before migration and breeding in this species. Diving efficiency and time spent feeding were quantified concomitantly for two subspecies that differ in the timing of their reproduction and migration. The foraging performance of female *S. m. dresseri* preparing for breeding and female *S. m. borealis* preparing for migration were compared with their male counterparts, which are known to achieve energy balance during these periods. Female *dresseri* spent 41% of their time feeding and made 404 dives daily, for a total of 169 min spent underwater each day. Female *dresseri* spent more time diving than did males by about one hour each day. There were no detectable differences in the foraging performances of male and female *borealis,* probably because the body mass of migrating females increased only slightly prior to migration. Hyperphagia in breeding female *dresseri* appears to be the main cause of increased body mass, although other mechanisms may play a role.

Key words: Common Eider, foraging performance, migration, reproduction, Somateria mollissima.

Quête Alimentaire Chez l'Eider à Duvet Avant la Migration Printanière et la Nidification: Est-Il Possible de Déceler un Phénomène d'Hyperphagie?

Résumé. Le quête alimentaire de l'Eider à duvet (*Somateria mollissima*) fut étudiée au printemps avant la migration et avant la nidification dans le but de déceler, s'il y a lieu, un phénomène d'hyperphagie chez cette espèce. Le temps passé à s'alimenter et l'efficacité de la plongée furent quantifiés simultanément pour deux sous-espèces qui diffèrent quant à leur chronologie de nidification et de migration. La quête alimentaire des femelles *S. m. dresseri,* se préparant pour la nidification, et des femelles *S. m. borealis,* se préparant pour la migration, fut comparée avec celle des mâles de chacune des sous-espèces respectives. Les mâles furent utilisés comme ''témoins'' puisqu'il y a des évidences que ces derniers maintiennent l'équilibre énergétique durant cette période. Les femelles *dresseri* ont passé en moyenne 41% de leur temps à s'alimenter et elles ont réalisé 404 plongeons quotidiennement, pour un total de 169 min. passées en plongée par jour, soit environ une heure de plus que les mâles. Il n'y avait pas de différences dans la performance de la quête alimentaire des femelles et des mâles *borealis,* probablement parce que les femelles n'emmagasinent que très peu de réserves avant leur départ pour la migration. En conclusion, un phénomène d'hyperphagie se manifeste chez la femelle *dresseri* bien que d'autres mécanismes d'accumulation de réserves peuvent jouer un rôle.

It is well known that birds can vary their body mass in the course of the annual cycle. Body mass and energy intake levels often increase in pre-breeding waterfowl because this phase of their annual cycle incurs additional costs for clutch formation and the growth of somatic tissues (Thomas 1988, Alisauskas and Ankney

---

Manuscript received 31 May 2000; accepted 11 April 2001.
[1] E-mail: magella_guillemette@uqar.qc.ca