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The Trematode Fauna of an Amazonian Antbird Community

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Parasites have been used as a tool to study the phylogeny of avian hosts (e.g. Baer and Mayr 1957). Differences between the parasite faunas of two host species could reflect differences in genetic susceptibility to the parasites or could be the result of differences in host feeding habits, habitat preferences, or behaviors. While studying habitat partitioning among 38 antbird species in eastern Ecuador, we collected the birds' trematode parasites. We were particularly interested to learn what ecological and taxonomic conclusions might be drawn from the trematode distributions among the hosts.

Methods and Materials.—Antbirds were collected from September 1975 through November 1976 in a relatively undisturbed moist tropical forest (sensu Holdridge 1967) in the vicinity of Limoncocha, a village in the Provincia Napo in east-central Ecuador (0°24'S, 76°37'W; 300 m elevation). Specimens of antbirds that served as hosts are housed at the Louisiana State University Museum of Zoology, Baton Rouge, and at the Universidad Catolica, Quito. Hosts were examined for parasites as soon as possible after being killed (never more than 8 h after death). We examined the digestive tract and associated organs, lungs, air sacs, body cavity, kidneys and associated ducts, and the female reproductive tract. Differences in parasite populations from different hosts were evaluated using a one-way analysis of variance (ANOVA).

Results.—Thirty-eight species of antbirds have been reported from Limoncocha, Ecuador (Table 1). We examined 358 specimens of 35 antbird species for parasites. Of these, 123 individuals of 27 species contained trematodes.

Eleven trematode species were extracted from the antbirds. The occurrence of these parasites ranged from rare (of incidental distribution and in small numbers), to intermediate (in scattered hosts and with larger numbers of individuals per host), and to common (widely distributed among hosts and found in large numbers). A list of parasites, hosts, incidence of infections, and infection sites is provided in Table 2.

Two trematode species were rare among the antbirds. Two immature specimens of Echinostomatidae were found in the kidneys of one *Myrmeciza hyperythra* host, and one gravid specimen of an undetermined species of Brachylaimidae was retrieved from one *Formicarius analis*.

Six parasites were intermediate in occurrence. *Lubens lubens* was found in *Gymnopithys, Thamnomanes,* and *Phlegopsis* hosts. The measurements of these specimens greatly overlapped. *Hylophylax* gall bladders contained a much smaller *Lubens,* which possibly could be a distinct species, but probably is a size variant of *L. lubens,* since *L. lubens* is a variable species (Travassos 1944; see Table 3). Although formerly unreported from Formicariidae, *L. lubens* is known from a wide variety of birds (Travassos et al. 1969).

Neodiplostomum ellipticum was found in moderate numbers in two individuals of *Percnostola leucaspis.* These trematode specimens fit the description for *N. ellipticum* given by Travassos et al. (1969). *Neodiplostomum ellipticum* is known from Brazil, Venezuela, and Jamaica from anis (*Crotophaga ani* and *C. major*) and the Squirrel Cuckoo (*Piaya cayana*), all of which occur at Limoncocha (Travassos et al. 1969, Yamaguti 1958).

The *Neodiplostomum* specimens from *Myrmeciza* (Table 4) were consistently much larger than *N. ellipticum* or any other Brazilian *Neodiplostomum* described by Travassos et al. (1969), with the exception of *N. tamarini,* a parasite of primates. However, *N. tamarini* has the posterior testis with a median lobe, a characteristic absent in the *Myrmeciza* trematode specimens. For these reasons, we believe the *Neodiplostomum* specimens found in *Myrmeciza* represent an undescribed species.

Brachylecithum rarum was found in the livers of *Formicarius* and *Chamaeza* hosts. Our material from *Formicarius* is similar to that figured in Travassos et al. (1969) and in Denton and Byrd (1951). Although the eggs in our sample appear to be relatively small, the measurements for all other features overlap those reported in the literature for *Brachylecithum rarum* (Table 5). These parasites were easily fragmented. We have no whole specimens from *Chamaeza;* the measurements of these fragmented worms suggest they are not statistically different from *Brachylecithum* in *Formicarius.* The parasite is known from Brazil, where it has been recovered from bile capillaries of various members of the order Passeriformes (Travassos et al. 1969), and from North America, where it has been found in Rufous-sided Towhees (*Pipilo erythrophthalmus;* Denton and Byrd 1951).

An unidentified species of *Leucochloridium* occurred in *Hylophylax, Myrmeciza, Myrmoborus,* and *Myrmotherula.* Although similar in shape to *L. parcum* from Brazil, our material is larger bodied, with a smaller acetabulum and oral sucker, and much smaller eggs (Table 6). Despite small sample sizes from different hosts, there is little variation among the specimens. We suspect that these specimens represent an undescribed species of *Leucochloridium.*

TABLE 1. Thirty-eight species of antbirds found at Limoncocha and their trematode infection rates.

No. birds		Infection		
Examined	Infected	rate (%)	Antbird species	Comments[a]
5	0	0	*Cercomacra cinerascens*	1
10	3	30	*Chamaeza nobilis*	3, 2
10	0	0	*Conopophaga aurita*	—
7	5	71	*Cymbilaimus lineatus*	—
19	7	37	*Formicarius analis*	1, 2
15	2	13	*F. colma*	1, 2
2	1	50	*Frederickena unduligera*	3
24	6	25	*Gymnopithys leucaspis*	1
17	3	18	*Hylophylax naevia*	1
12	1	8	*H. poecilonota*	1
11	2	18	*Hypocnemis cantator*	1
1	0	0	*Myrmeciza atrothorax*	—
7	2	29	*M. fortis*	3
10	3	30	*M. hyperythra*	1
10	1	10	*M. melanoceps*	4
15	8	53	*Myrmoborus myotherinus*	1
4	1	25	*Myrmothera campanisona*	1, 2
15	3	20	*Myrmotherula axillaris*	1
—	—	—	*M. brachyura*	b
1	0	0	*M. erythrura*	1
21	5	24	*M. hauxwelli*	1
1	0	0	*M. longipennis*	1
7	3	43	*M. menetriesii*	1
12	4	33	*M. ornata*	1
3	2	67	*M. schisticolor*	5
—	—	—	*M. sunensis*	c
1	0	0	*M. surinamensis*	5
4	0	0	*Neoctantes niger*	—
19	11	58	*Percnostola leucostigma*	1
10	7	70	*Phlegopsis erythroptera*	3
20	10	50	*P. nigromaculata*	1
8	1	12	*Pygiptila stellaris*	1
5	1	20	*Sclateria naevia*	1
1	0	0	*Taraba major*	4
21	20	95	*Thamnomanes ardesiacus*	1
17	10	59	*T. caesius*	1
—	—	—	*Thamnophilus murinus*	d
13	1	8	*T. schistaceus*	1
358	123	34	Total	

[a] (1) Bird species common in primary forest understory. (2) Groundwalker. (3) Uncommon in primary forest understory. (4) Common in secondary growth. (5) Rare in primary forest, restricted to vicinity of water. (b) One specimen; not searched. (c) Two specimens; not searched. (d) Not observed, but previously reported from Limoncocha (Pearson 1972).

Urotocus fusiformis was intermediate in occurrence. Specimens of this species were found in *Chamaeza*, *Formicarius*, and *Myrmothera*. Most dimensions of our material fall within the parameters for *Urotocus fusiformis*, although our specimens are somewhat smaller in length and width. Travassos et al. (1969) described one specimen of *Paraurotocus* [=*Urotocus*] *fusiformis* from a House Sparrow (*Passer domesticus*) in Brazil, but gave no internal measurements. Although the *Urotocus* populations found in the different antbird hosts appear to be statistically distinct, with those in *Chamaeza nobilis* largest and in *Formicarius analis* smallest, there is overlap between minima and maxima of most variables. The exception is a single *Urotocus* taken from one *Myrmothera campanisona*. This individual is larger than the other specimens (Table 7). Furthermore, it is from the gall bladder, rather than Bursa of Fabricius, where all other *Urotocus* specimens were found. Because this specimen lies within the range described by McIntosh (1935), we conclude that one variable species is involved.

Although *Prosthogonimus cuneatus* is a cosmopolitan species found in a wide variety of birds (Yamaguti 1958), we recorded it from *Chamaeza*, *Gymnopithys*, *Percnostola*, *Sclateria*, and *Thamnomanes*. All the antbirds with this trematode had single-worm infections.

TABLE 2. Summary of trematode (names in bold) infections of Limoncocha antbirds. Incidence is total number of parasites found in indicated number of infected hosts.

Host	Incidence	Site
	Echinostomatidae sp.	
Myrmeciza hyperythra	2 in 1	Kidney
	Brachylaimidae sp.	
Formicarius analis	1 in 1	Intestine
F. colma	1 in 1	Intestine
	Lubens lubens	
Gymnopithys leucaspis	3 in 1	—[a]
Hylophylax poecilonota	1 in 1	Gall bladder
Pygptila stellaris	1 in 1	Bile duct
Phlegopsis erythroptera	3 in 2	Gall bladder, liver
Thamnomanes ardesiacus	5 in 3	Bile duct
	Neodiplostomum ellipticum	
Percnostola leucaspis	29 in 2	Intestine
	***Neodiplostomum* sp.**	
Myrmeciza fortis	8 in 1	—
	Brachylecithum rarum	
Formicarius analis	27 in 4	Liver ducts
Chamaeza nobilis	6 in 1	Liver
	***Leucochloridium* sp.**	
Hylophylax naevia	1 in 1	—
Myrmeciza fortis	2 in 1	—
Myrmoborus myotherinus	3 in 2	Kidney
Myrmotherula hauxwelli	2 in 1	Intestine
	Urotocus fusiformis	
Chamaeza nobilis	5 in 1	Bursa of Fabricius
Formicarius analis	15 in 1	Bursa of Fabricius
F. colma	55 in 1	Bursa of Fabricius
Mymothera campanisona	1 in 1	Gall bladder
	Prosthogonimus cuneatus	
Chamaeza nobilis	1 in 1	Kidney
Gymnopithys leucaspis	1 in 1	Bursa of Fabricius
Percnostola leucostigma	1 in 1	Bursa of Fabricius
Sclateria naevia	1 in 1	Bursa of Fabricius
Thamnomanes caesius	1 in 4	Bursa of Fabricius
	Zonorchis delectans	
Gymnopithys leucaspis	7 in 4	Gall bladder
Myrmeciza hyperythra	1 in 1	Gall bladder
Percnostola leucostigma	12 in 7	Liver, gall bladder
Cymbilaimus lineatus	6 in 2	Liver
Hypocnemis cantator	1 in 1	Kidney
Myrmoborus myotherinus	8 in 4	Bile duct, gall bladder
Myrmotherula axillaris	4 in 1	Gall bladder
M. hauxwelli	12 in 4	Gall bladder, liver
M. ornata	4 in 2	Bile duct, liver
M. schisticolor	7 in 2	Gall bladder, liver, bile duct
Phlegopsis erythroptera	13 in 5	Gall bladder
P. nigromaculata	23 in 10	Gall bladder, liver
Thamnomanes ardesiacus	38 in 16	Gall bladder
T. caesius	15 in 6	Gall bladder, kidney
	Tanaisia bragai	
Formicarius analis	2 in 2	Kidney
Frederickena undiligera	10 in 1	Kidney
Gymnopithys leucaspis	2 in 1	—
Hylophylax naevia	9 in 2	Kidney

TABLE 2. Continued.

Host	Incidence	Site
Myrmeciza hyperythra	3 in 1	Kidney
M. melanoceps	3 in 1	Kidney
Percnostola leucostigma	4 in 3	Kidney
Cymbilaimus lineatus	12 in 2	Kidney
Hypocnemis cantator	16 in 1	Kidney
Myrmoborus myotherinus	20 in 2	Kidney
Myrmotherula axillaris	8 in 2	Kidney
M. menestresii	14 in 3	Kidney
M. ornata	4 in 2	Kidney
Thamnomanes ardesiacus	37 in 5	Kidney, oviduct
T. caesius	15 in 1	Kidney
Thamnophilus schistaceus	12 in 1	Kidney

[a] Site not recorded.

We judged two species of trematodes to be common parasites of Limoncocha antbirds given that they were widely distributed among the antbirds and found in large numbers within individual hosts. *Zonorchis delectans* was found in the gall bladder and/or liver of 14 species of antbirds. With the exception of egg width, which is small in our specimens, our mean data fit in the description of *Z. delectans* given by Travassos (1944; Table 8). The parasite is known to occur in bile ducts of a variety of species, including, significantly, *Formicarius "ruficeps,"* now considered a subspecies of *F. colma* (Meyer de Schauensee 1966). The somewhat smaller eggs of our specimens support Travassos' (1944) suggestion that *Z. mazzai* and *Platynosomum furnarii* are synonyms for *Z. delectans*. Despite their ubiquity in the antbird hosts, the 149 specimens from 14 host species show a remarkable consistency in size. All 14 of the antbird species represent new host records for the trematode.

Tanaisia bragai is the other common trematode of the antbirds. Specimens were found in 16 antbird species. Measurements of *Tanaisia* specimens taken from the antbirds agree closely with those given by Byrd and Denton (1950) for *T. bragai* (Table 9). This similarity is surprising given that all of the antbird species represent previously unreported hosts for the trematode. Normally an inhabitant of the kidney, one *Tanaisia* was found in an oviduct of *Thamnomanes ardesiacus*.

Discussion.—Haverschmidt (1968) found that the major components of antbird species' diets in Surinam were members of the Coleoptera, Hymenoptera, Orthoptera, Arachnoidea, Hemiptera, Homoptera, and Lepidoptera, as well as a variety of other insect orders; mollusks also were commonly eaten. In addition to various insect remains, we occasionally noted spiders and small snails in antbird stomach contents. Any of these taxa could serve as intermediate hosts for the antbird trematodes. The overall trematode infection rate for the antbirds in our study was 34%. Infection rates ranged from 95% of 21 *Thamnomanes ardesiacus* to 8% of 13 *Thamnophilus schistaceus* and 0% of 10 *Conopophaga aurita* (Table 1).

Parasites have been used to indicate phylogenetic relationships among birds. At a symposium led by Baer and Mayr (1957), Clay suggested that feather lice

TABLE 3. Comparison of measurements (in microns) from Travassos' (1944) description of *Lubens lubens* from *Myiozetes similis* with those from present study. Differences in sample sizes due to damaged specimens or hidden organs.

Variable	Travassos	Present study	
		Average (range; *n*)	*Hylophylax*
Length	2,200–4,200	4,700 (2,900–5,800; 9)	2,500
Width	1,600–4,300	2,000 (1,600–2,500; 10)	1,300
Acetabulum diameter	370–490	454 (300–590; 10)	300
Oral sucker diameter	310–450	457.5 (350–600; 10)	280
Pharynx diameter	120–160	163 (120–190; 8)	80
Ovary length	200–400	250 (200–310; 10)	230
Ovary width	410–660	330 (250–420; 9)	180
Mehlis gland diameter	120–240	179.5 (110–250; 8)	70–80
Vitellaria from posterior	410–1,500	2,070 (1,080–3,130; 10)	800
Egg length	30–32	27 (14–35; 9)	28
Egg width	20–23	17 (14–21; 9)	14

TABLE 4. Comparison of measurements (in microns) from Travassus et al.'s (1969) description of *Neodiplostomum ellipticum* with those from present study.

Variable	Travassos et al.	Present study[a]
Length	770–1,500	1,070 (890–1,280; 18)
Acetabulum length	36–86	75 (56–98; 28)
Acetabulum width	40–95	80 (56–126; 28)
Oral sucker length	38–86	89 (70–112; 25)
Oral sucker width	38–97	85 (70–119; 25)
Pharynx length	40–72	51 (42–70; 24)
Pharynx width	17–49	39 (28–49; 24)
Egg length	83–102	89 (63–105; 25)
Egg width	50–65	52 (42–77; 25)

[a] Average with range and sample size in parentheses.

TABLE 5. Comparison of measurements (in microns) of *Brachylecithum rarum* by Travassos (Travassos 1944, Travassos et al. 1969) and Denton and Byrd (1951) with those from present study.

Variable	Travassos	Denton and Byrd (1951)	Present study[a]
Length	4,200–4,500	4,500–6,900	4,865.8 (3,871–6,454; 8)
Width	240–390	300–490	243.7 (126–406; 27)
Acetabulum diameter	260–340	280–380	232 (105–315; 17)
Oral sucker diameter	240–340	290–410	212 (105–406; 14)
Pharynx diameter	30–38	80–110	51.6 (35–70; 11)
Testis diameter	280–330	170–320	274 (112–560; 24)
Ovary diameter	120–210	110–210	160 (84–238; 27)
Vitellaria from posterior	2,100–2,600	—	1,976.8 (1,330–2,688; 15)
Egg length	41–49	44–57	37.1 (28–49; 33)
Egg width	26–30	23–33	18.9 (14–21; 33)

[a] Average with range and sample size in parentheses.

TABLE 6. Comparison of measurements (in microns) from Travassos' (1944) description of *Leucochloridium parcum* with those from present study.

Variable	Travassos	Present study[a]
Length	1,000–2,100	2,716.0 (2,303–3,325; 6)
Width	700–1,000	1,006.6 (798–1,162; 5)
Acetabulum diameter	530	486.5 (476–511; 7)
Oral sucker diameter	500	418.5 (183–588; 7)
Pharynx length	190	126 (126; 7)
Pharynx width	120	133 (133; 7)
Egg length	28	15.4 (14–21; 5)
Egg width	17	7 (7; 5)

[a] Average with range and sample size in parentheses.

TABLE 7. Comparison of measurements (in microns) from McIntosh's (1935) original description of *Urotocus fusiformis* with those from present study.

Variable	McIntosh	Present study Average (range; *n*)	*Myrmothera*
Length	5,000	2,614.8 (1,736–4,004; 58)	4,501
Width	1,450	548.5 (336–931; 70)	1,099
Acetabulum diameter	Absent	Absent	Absent
Oral sucker length	70	67.5 (56–91; 59)	Hidden
Oral sucker width	100	80.2 (63–98; 59)	Hidden
Pharynx length	46	48.2 (35–63; 62)	Hidden
Pharynx width	70	57.7 (35–84; 62)	Hidden
Ovary length	245–260	157.4 (84–287; 68)	280
Ovary width	350–380	173.2 (105–301; 68)	301
Egg length	28	23 (14–35; 75)	28
Egg width	20	14.4 (14–21; 75)	14
Anterior testis length	285–320	180 (119–315; 56)	385
Anterior testis width	300–370	181.2 (98–280; 56)	413
Posterior testis length	212–290	184.9 (112–301; 62)	483
Posterior testis width	300–320	179.3 (112–301; 62)	364

TABLE 8. Comparison of measurements (in microns) from Travassos' (1944) description of *Zonorchis delectans* with those from present study.

Variable	Travassos	Present study[a]
Length	2,000–5,800	3,456.2 (1,806–5,740; 110)
Width	500–2,600	734.5 (217–1,274; 146)
Acetabulum diameter	300–640	424 (203–644; 151)
Oral sucker diameter	160–480	201 (70–399; 146)
Testis diameter	100–530	166.5 (35–343; 132)
Ovary length	160–420	201 (13–1,645; 146)
Ovary width	130–270	157.8 (70–266; 146)
Vitellaria from posterior	400–1,300	1,416 (539–3,066; 128)
Egg length	34–36	32.2 (14–42; 149)
Egg width	22–24	18.1 (10.5–161; 149)

[a] Average with range and sample size in parentheses.

TABLE 9. Comparison of measurements (in microns) from Byrd and Denton's (1950) description of *Tanaisia bragai* with those from present study.

Variable	Byrd and Denton[a]	Present study[b]
Length	1,990 (1,620–2,550)	2,183.8 (1,267–3,325; 139)
Width	420 (320–530)	380.4 (168–539; 155)
Oral sucker length	170 (130–200)	215.2 (112–280; 151)
Oral sucker width	190 (140–230)	216.4 (112–273; 151)
Pharynx length	60 (40–80)	60.1 (35–91; 148)
Pharynx width	80 (60–90)	70.9 (14–98; 148)
Ovary length	180 (150–200)	162.9 (63–252; 149)
Ovary width	140 (100–190)	132.5 (77–224; 149)
Egg	120 (90–150)	161.9 (70–273; 161)
Right testis length	100 (70–150)	103.7 (42–175; 141)
Right testis width	130 (90–180)	163.6 (70–266; 141)
Left testis length	110 (80–150)	104.2 (56–182; 142)
Left testis width	—	161.9 (70–273; 142)

[a] Average with range in parentheses.
[b] Average with range and sample size in parentheses.

TABLE 10. Distribution of trematodes among ground-foraging species (*Chamaeza, Formicarius analis, F. colma,* and *Myrmothera campanisona*) as compared with other antbird species in community. Number of host species infected, with percent of infected species within each group given in parentheses.

	No. antbird species	
Parasite	Ground-foraging species	Other species
Zonorchis	0 (0)	14 (61)
Tanaisia	1 (25)	15 (65)
Lubens	0 (0)	5 (22)
Leucochloridium	0 (0)	4 (17)
Prosthogonimus	1 (25)	4 (17)
Diplostomatidae	0 (0)	2 (9)
Echinostomatidae	0 (0)	1 (4)
Urotocus	4 (100)	0 (0)
Brachylecithum	2 (50)	0 (0)
Brachylaimidae	2 (50)	0 (0)

(Mallaphaga) ally ostriches with rheas and also flamingos with geese; Manter maintained that Digenea do not show high host specificity (at least in fishes) at the level of definitive host, and that ecological convergence obscures phylogenetic relationships. At the same symposium, Dubois' attempt to ally hawks with owls on the basis of shared trematodes was criticized by Mayr, since both groups take the same prey items, which presumably contain the same parasites.

Despite niche partitioning (see Tallman 1979) and a wide variety of feeding behaviors, ranging from flycatching in *Thamnomanes* to gleaning in *Myrmotherula,* and leaf tossing in *Formicarius* (see Campbell and Lack 1985), the antbirds of Limoncocha supported a relatively homogeneous assemblage of trematodes. Of the 27 antbird species with trematodes, 23 species harbored either *Zonorchis* or *Tanaisia* (10 had both). Almost all of the other infections were incidental in nature, with a few trematodes being collected from a few hosts. Important exceptions were the genera *Brachylecithum* and *Urotocus,* as well as the family Brachylaimidae; these were restricted to bird genera that are ground walkers. Interestingly, these parasites were absent from species that fed on the ground and in low vegetation (*Phlegopsis* or *Gymnopithys;* Table 10). This difference in trematode distribution is dramatic and statistically significant (one-way ANOVA; $P < 0.001$); it can be explained in two ways. Either these ground antbirds are feeding on prey items not taken by other antbird species or, if they do feed on the same prey, these two groups of antbirds are not susceptible to the same parasites. Regardless of the cause for this difference, our trematode data show that the ground antbirds are a distinct group. Division of antbirds into two groups on the basis of trematode distribution is consistent with morphological studies (Ames 1971, Feduccia and Olson 1982) and DNA-hybridization work by Sibley and Ahlquist (1990) that place the two groups of antbirds in separate families, Formicariidae for ground antbirds and Thamnophilidae for typical antbirds.

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Nocturnal Behavior of Breeding Trumpeter Swans

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The study of nocturnal waterfowl behavior has received little attention, in part because researchers have usually assumed night to be a time of little or no activity (Baldassarre et al. 1988, Jorde and Owen 1988, Paulus 1988). The few studies that have focused on nocturnal activity have shown a surprising amount of behavioral variation (Linsell 1969, Nilsson 1970, Swanson and Sargeant 1972, Ydenberg et al. 1984). Waterfowl studies that included evaluations of nighttime activity have revealed a variety of nocturnal behaviors (Raveling et al. 1972, Ebbinge et al. 1975, Tamisier 1976, Pedroli 1982, Aldrich and Raveling 1983, Moulton and Weller 1984, Paulus 1984, Madsen et al. 1989). However, none of these studies focused specifically on nocturnal behavior.

Differences in nocturnal behavior between waterfowl may be due to the great variety of environmental and physiological stimuli encountered by various species (Jorde and Owen 1988). Nilsson (1970), for example, found that three of nine species of diving ducks studied in Sweden were predominantly nocturnal feeders, while the other six were diurnal; nocturnal feeders mostly fed on sessile foods while the diurnal birds ate more mobile prey. Predation pressure is less intense at night and may encourage nocturnal feeding in some ducks (Tamisier 1974, Paulus 1984). Nocturnal feeding also might be important to birds that are energetically stressed, such as prelaying females or birds undergoing wing molt (Jorde and Owen 1988). These examples illustrate the importance of including nocturnal observations when studying a species' behavior and ecology. Conclusions based solely on diurnal data will not represent diel patterns and might lead to a misinterpretation of diurnal activities (Baldassarre et al. 1988, Jorde and Owen 1988).

Nocturnal feeding and other behaviors have been documented in wintering Mute Swans (*Cygnus olor*), Bewick's Swans (*C. columbianus bewickii*), and Trumpeter Swans (*C. buccinator*; Owen and Cadbury 1975, McKelvey and Verbeek 1988). Nocturnal behavior of breeding swans is unknown. Cooper (1979) and Hampton (1981) used electronic monitoring devices (Cooper and Afton 1981) to quantify the presence of incubating female Trumpeter Swans at the nest during the nocturnal period, but nighttime behavior of males, nonincubating females, and cygnets was not evaluated.

We studied the nocturnal behavior of Trumpeter Swans breeding in Wyoming and Idaho in 1991. Our objective was to quantify nocturnal behavior of breeding Trumpeter Swans through direct observations using night-vision equipment. Specific questions addressed were: (1) Are breeding swans active at night? (2) If nocturnal activity is occurring, is it correlated with environmental and physiological factors? (3) What is the relative importance of diurnal and nocturnal periods to breeding swans?

Methods.—Staging and breeding swans were observed on wetlands in: Wyoming at Yellowstone National Park; Idaho in the Ashton and Island Park Districts of the Targhee National Forest, in Harriman State Park, and on the Sand Creek State Wildlife Refuge. The ecological aspects of this region have been described by Banko (1960), Shea (1979), and Maj (1983).

Observation blinds were erected at staging areas and on nearby hills that overlooked four swan breeding territories. All blinds were hidden by vegetation and were located 100 to 250 m from the nest mounds. Observations also were recorded from vehicles parked on roads overlooking two other territories. We observed each territory every two to four days from prelaying through brood rearing. We used spotting scopes (60×) by day and Noctron-V Model 9878 light-intensifying night-vision scopes (Varo Inc., Electron Devices Division, Garland, Texas) at night. Night-

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