

- GRIER, J. W., AND T. BURK. 1992. Biology of animal behavior. Mosby Year Book, St. Louis, Missouri.
- HARLOW, R. F., AND M. R. LENNARTZ. 1983. Interspecific competition for Red-cockaded Woodpecker cavities during the breeding season in South Carolina. Pages 41–43 in Red-cockaded Woodpecker Symposium II (D. A. Wood, Ed.). Florida Game and Freshwater Fish Commission, Tallahassee.
- INGOLD, D. J. 1994. Influence of nest-site competition between European Starlings and woodpeckers. *Wilson Bulletin* 106:227–241.
- JACKSON, J. A. 1978. Competition for cavities and Red-cockaded Woodpecker management. Pages 103–112 in Management techniques for preserving endangered species (S. A. Temple, Ed.). University of Wisconsin Press, Madison.
- KAPPES, J. J., JR., AND L. D. HARRIS. 1995. Interspecific competition for Red-cockaded Woodpecker cavities in Apalachicola National Forest. Pages 389–393 in Red-cockaded Woodpecker: Recovery, ecology and management (D. L. Kulhavy, R. G. Hooper, and R. Costa, Eds.). Center for Applied Studies, College of Forestry, Stephen F. Austin State University, Nacogdoches, Texas.
- LABRANCHE, M. S., AND J. R. WALTERS. 1994. Patterns of mortality in nests of Red-cockaded Woodpeckers in the sandhills of southcentral North Carolina. *Wilson Bulletin* 106:258–271.
- LIGON, J. D. 1970. Behavior and breeding biology of the Red-cockaded Woodpecker. *Auk* 87:255–278.
- LIGON, J. D. 1971. Some factors influencing numbers of the Red-cockaded Woodpecker. Pages 30–43 in The ecology and management of the Red-cockaded Woodpecker (R. L. Thompson, Ed.). Bureau of Sport Fisheries and Wildlife and Tall Timbers Research Station, Tallahassee, Florida.
- LOEB, S. C. 1993. Use and selection of Red-cockaded Woodpecker cavities by southern flying squirrels. *Journal of Wildlife Management* 57:329–335.
- MACARTHUR, R. H. 1972. Geographical ecology: Patterns in the distribution of species. Harper and Row, New York.
- MARTIN, T. E. 1986. Competition in breeding birds: On the importance of considering processes at the level of the individual. *Current Ornithology* 4:181–210.
- NEAL, J. C., W. G. MONTAGUE, AND D. D. JAMES. 1992. Sequential occupation of cavities by Red-cockaded Woodpeckers and Red-bellied Woodpeckers in the Quachita National Forest. *Proceedings of the Arkansas Academy of Science* 46:106–108.
- RUDOLPH, D. C., R. N. CONNER, AND J. TURNER. 1990. Competition for Red-cockaded Woodpecker roost and nest cavities: Effects of resin age and entrance diameter. *Wilson Bulletin* 102:23–36.
- SHORT, L. L. 1979. Burdens of the picid hole-excavating habit. *Wilson Bulletin* 91:16–28.
- TROETSCHLER, R. G. 1976. Acorn Woodpecker breeding strategy as affected by Starling nest-hole competition. *Condor* 78:151–165.
- WALTERS, J. R. 1990. The Red-cockaded Woodpecker: A primitive cooperative breeder. Pages 69–101 in Cooperative breeding in birds: Long-term studies of ecology and behavior (P. B. Stacey and W. D. Koenig, Eds.). Cambridge University Press, Cambridge, United Kingdom.
- WALTERS, J. R. 1991. Application of ecological principles to the management of endangered species: The case of the Red-cockaded Woodpecker. *Annual Review of Ecology and Systematics* 22:505–523.
- WINKLER, H., D. A. CHRISTIE, AND D. NURNEY. 1995. Woodpeckers: A guide to the woodpeckers of the world. Houghton Mifflin, Boston.

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Interspecific Aggression in *Formicarius* Antthrushes? The View from Central Amazonian Brazil

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Two species of terrestrial antbirds, the Black-faced Antthrush (*Formicarius analis*) and the Rufous-capped Antthrush (*F. colma*), are sympatric through much of

lowland Amazonia (Ridgely and Tudor 1994). In Manu National Park, in southeastern Peru, *F. analis* (58 g) is behaviorally dominant to the smaller *F. colma* (49 g; Robinson and Terborgh 1995). *Formicarius analis* also is much more common and has smaller territories. Robinson and Terborgh suggested that the coexistence of

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these two species in Peru is possible because the large territories of *F. colma* allow it to avoid coming into contact with *F. analis*, even though their territories sometimes overlap. Here, I report observations and experimental results for these species near Manaus, Brazil. At Manaus, playback experiments show no evidence of interspecific aggression. Relative abundance also varies between the sites. Near Manaus, *Formicarius colma* is more common and has smaller territories than *F. analis*.

Territorial birds typically defend a breeding territory against intrusion by conspecifics, but only rarely are responsive to heterospecific intruders. Experimental and observational evidence indicates that interspecific aggression is usually directed only to one or two congeners that are ecologically similar (Orians and Willson 1964, Murray 1971, Rice 1978, Catchpole and Leisler 1986, Prescott 1987). Presumably, this aggression results from competition between closely related species, although the extent to which it is an adaptive trait has been debated (Cody 1974, Murray 1981). For closely related species that partition a habitat gradient, interspecific aggression may occur in that part of the gradient that is suitable for both species (Murray 1971). Nectar-feeding birds also exhibit strong interspecific territoriality, but this is based on short-term defense of a food resource, not defense of a multipurpose territory (e.g. Feinsinger 1976, Murray 1981).

Based on a series of playback experiments with 27 species pairs, Robinson and Terborgh (1995) concluded that interspecific territoriality is common in birds using a primary successional gradient in Manu National Park (hereafter "Peru"). The response was strongest in species pairs that had non-overlapping territories, although in some cases it occurred between species with overlapping territories. In most cases the response was asymmetrical, with the larger species responding much more aggressively to heterospecific playback than the smaller species. Robinson and Terborgh concluded that by virtue of their size advantage, the larger species excluded smaller congeners from more productive habitats and forced them into earlier successional areas.

Robinson and Terborgh (1995) found that *F. analis* responded aggressively to playback of *F. colma* vocalizations, whereas *F. colma* moved away from playback of *F. analis* vocalizations. In the case of this species pair, the subordinate species (*F. colma*) was not restricted to earlier successional areas, but was less common and had larger territories than *F. analis*, presumably to avoid interspecific interference (Robinson and Terborgh 1995, Terborgh pers. comm.). Although many studies of interspecific territoriality have been done with congeners that are very similar in appearance or vocalizations, the two *Formicarius* have very different appearances, call notes, and songs (Ridgely and Tudor 1994). Thus, they are unlikely to be confused with each other, either by human observers or by the birds themselves (see Murray 1971, 1976).

These two species also occur in the forests near Ma-

naus, in central Amazonian Brazil. As in Peru, *F. analis* (62 g) is much larger than *F. colma* (46g; Bierregaard 1988). Unlike in Peru, however, *F. colma* is much more common than *F. analis* based on mist-net capture rate in undisturbed forest (2.8 vs. 0.3 captures per 1,000 net h; Stouffer and Bierregaard 1995). This difference between two well-studied sites prompted me to examine interspecific interactions near Manaus. I also was interested in measuring abundance with a method other than mist nets, which can be an inefficient and possibly biased technique for terrestrial birds (see Remsen and Good 1996). To make the results from the two sites comparable, I followed the methods of Robinson and Terborgh (1995) as closely as possible. First, I quantified abundance of the two species. Second, I examined the extent of territorial overlap between them. Third, I used playback experiments to determine the degree of interspecific aggression between the two species.

Methods.—This study was conducted in reserve 1501 of the Biological Dynamics of Forest Fragments Project, in terra firme forest 80 km north of Manaus, Brazil (2°30'S, 60°00'W). Reserve 1501 is within continuous forest, bordered to the south and southeast by a narrow road and several small, abandoned farms. To the west, the nearest disturbance is a cattle ranch about 18 km away. To the north, the forest stretches with almost no disturbance for hundreds of km (see Lovejoy and Bierregaard 1990, Bierregaard et al. 1992).

I surveyed birds in a 100-ha plot within reserve 1501 between June and August 1995. The breeding season of *F. analis* at Manaus is unknown, but *F. colma* may breed from about February to May (based on increased singing and parents accompanied by begging juveniles). The area has a gridded trail system, with trails every 100 m. As part of a larger study of terrestrial insectivorous birds, I spot-mapped *F. colma* and *F. analis* in the plot on 36 days, systematically surveying the plot between 0530 (about 30 min before dawn) and 0800 and between 1700 and 1800 (dusk). Although these were the times of peak vocal activity, I also recorded opportunistic detections at other times, except for radio-tagged birds that I heard or saw while I was locating them (see below). For each *Formicarius* detected, I noted the time, the type of detection (bird seen, bird heard calling, or bird heard singing), the location, the number of calls or songs, and any response from conspecifics or congeners. To reduce the possibility of overlooking birds in the plot, I used tape playback for each species in areas where no birds were detected.

Four *F. colma* and four *F. analis* were captured and outfitted with radio transmitters from June to August 1995 and June and July 1996. Birds were captured by using playback of conspecific calls and songs to lure them into mist nets. The birds were outfitted with 1.5-g radio transmitters (Wildlife Materials SOPB 2028) mounted with backpacks or glue. These birds were located one to four times daily, with a minimum of two hours between locations. All

data from radio-tagged birds were kept separate from spot-mapping data. I used the algorithms in Ranges IV software (Kenward 1990) to estimate territory size of the radio-tagged birds.

I conducted playback experiments with 11 individuals of each species in 1995 and 1996. Each territory was sampled only once. Because of the low density of *F. analis* (see Results), it was necessary to search for birds outside the plot. I hoped to find birds that were spontaneously singing before the playback trial, but this proved difficult for both species. Of the 11 *F. colma* used in the experiments, one was singing, five were calling, two were silent radio-tagged birds, one was seen, and two were induced to call by playback of *F. colma* calls and songs. For *F. analis*, eight birds were singing, one was a silent radio-tagged bird, and two were induced to call or sing by conspecific playback. For the birds that were located by conspecific playback, I stopped playback immediately when the bird responded, then moved toward the area where I heard the bird. In all cases these birds stopped vocalizing, but I waited several minutes before beginning the playback trials.

I performed playback trials following the methods of Robinson and Terborgh (1995). First, I played a tape of heterospecific calls and songs for 5 min. During this period, I remained partially concealed at least 5 m from the recorder and noted any vocalizations or movements by the target bird. Following the heterospecific playback, I played conspecific calls and songs for 5 min. As before, I noted any vocalizations or movements by the target bird. The responses to both trials were scored following the criteria listed in Table 1, which follow Robinson and Terborgh (1995). I modified their scale slightly to reflect the behavior of anthruses. For vocalization frequency, the important response is the change in vocalization frequency from before the trial, so it is impossible to quantify the frequency of vocalization scales, especially for ranks 3 to 8. For example, a bird that called three times in 1 min before the trial and six times in 1 min during the trial would get a score of at least 7. A bird that called six times in 1 min before the trial and six times in 1 min during the trial could receive a score as low as 4. In practice, the combination of vocalizations and movements made it fairly easy to assign the scores.

Differences between species in response to heterospecific vocalizations were tested with a Mann-Whitney *U*-test. This tested the null hypothesis that the species do not differ in response to heterospecific playback. I analyzed differences in response to conspecific and heterospecific playback within individuals with a Wilcoxon signed-rank test for each species. This tested the null hypothesis that birds responded equally to conspecific and heterospecific vocalizations. Tapes were broadcast with a Marantz PMD 222 recorder or a Panasonic personal recorder, in either case amplified through an Archer remote speaker. I made the contin-

TABLE 1. Ranks used to score response to playback experiments by anthruses in Brazil.

Rank	Response
10	Approach to <1 m, or vocalize nearly constantly
9	Approach to <5 m, or vocalize repeatedly
8	Approach to 6 to 15 m, displaying agitation, or vocalize frequently
7	Approach to 15 to 30 m, with no indication of agitation, or increase vocalization rate
6	Gradually approach to 30 to 40 m, continue vocalizing at same rate
5	Make no changes in position relative to speaker, continue vocalizing at same rate
4	Move away gradually, with net movement away from speaker, continue vocalizing at same or slightly decreased rate
3	Move away gradually but directionally, or continue vocalizing, but at markedly decreased rate
2	Move away rapidly and vocalize no more than twice
1	Move away immediately and stop vocalizing.

uous-loop tapes for playback from vocalizations I recorded at the study site using the same tape recorder and a Sennheiser ME66 microphone.

Results.—I recorded 136 spot-map registrations of *F. colma* and 19 of *F. analis* in the 100-ha plot (Fig. 1). *Formicarius colma* was recorded in 75 ha; several of the areas where it was not recorded, especially in the northeastern part of the plot, included areas of long, steep slopes with large treefalls. *Formicarius analis* was recorded in 12 ha concentrated in two corners of the plot (Fig. 1). Although I used tape playback throughout the plot for *F. analis*, no birds responded except where I had already spot-mapped birds that vocalized spontaneously.

From the observed frequencies of occurrence (i.e. 0.75 for *F. colma* and 0.12 for *F. analis*), the interaction of the two species can be examined. If their distribution were influenced by interspecific territoriality, then the species would be expected to occur in different areas of the plot without overlap. Alternatively, if they associated positively, then they would be expected to occur in the same areas. The empirical result, however, showed neither a negative nor a positive association. Territories of the two species overlapped in nine ha, which is exactly the overlap that would be expected if they were distributed independently of each other ($0.75 \times 0.12 \times 100$ ha).

It was difficult to determine territorial boundaries based on territorial interactions of *F. colma*, which I never heard countersinging. Both sexes called frequently, but I seldom heard songs. Based on radio-tagged birds, I suspect that pair members sometimes

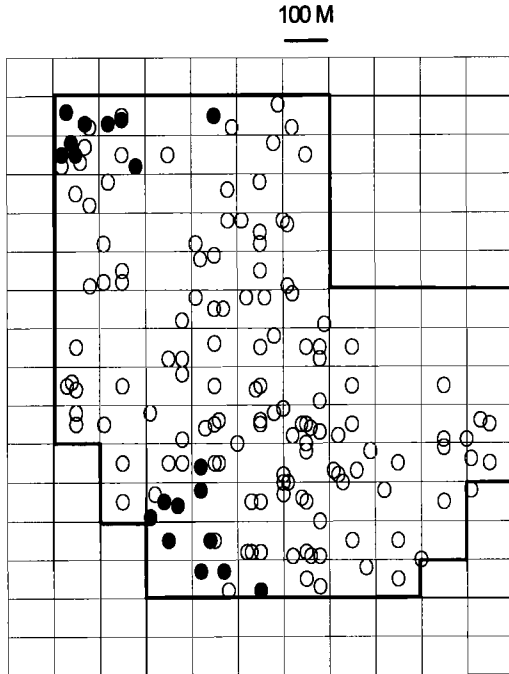


FIG. 1. Spot-map registrations of *Formicarius colma* (open circles) and *F. analis* (closed circles) in a 100-ha plot of continuous forest near Manaus, Brazil. Bold lines show outline of plot; faint lines indicate trails, which are separated by 100 m.

foraged >100 m apart. Thus, it was often impossible to determine if birds exchanging calls were paired. I estimated territory size for four radio-tagged *F. colma* within the plot. Each bird was located at least 64 times on a minimum of 21 days. Based on a minimum convex polygon algorithm, territory sizes ranged from 5.2 to 7.7 ha. These estimates are highly dependent on sample size, so I also calculated territory size with a nonparametric kernel method (Worton 1989, White and Garrott 1990); the 95% isopleths ranged from 4.8 to 11.0 ha. In practice, this technique reduces the territory-size estimate if the minimum convex polygon is distended by outliers, but increases it if points are more uniformly distributed. For *F. colma*, additional sampling after about 20 days did not lead to a significant increase in estimated territory size (i.e. area reached a plateau). Based on the mean of the highest (11.0 ha) and lowest (4.8 ha) estimates, or 7.9 ha, the 75 ha occupied in the plot represented approximately 9.5 *F. colma* territories per 100 ha. With one pair per territory, the estimated biomass of *F. colma* was 874 g per 100 ha.

Formicarius analis neighbors countersang on two occasions, once in the northwest corner of the plot and once in the southwest corner. Thus, the two clusters of registrations each represent two territories

(Fig. 1). In the northwest corner, both territories shown in Figure 1 extended well outside of the plot. In the southwest corner, one territory extended slightly outside of the plot. The other, the territory of one of the radio-tagged *F. analis*, was mostly within the plot. Three *F. analis* were radio-tagged in 1996. One was the bird in the northwest corner of the plot. Another was a bird in the central part of the plot, an area where *F. analis* was absent in 1995. The third was about 500 m west of the plot. Each was located at a least 22 times on a minimum of 7 days. Minimum convex polygon estimates varied from 5.9 to 21.2 ha, and kernel estimates of the 95% isopleths were 7.9 to 37.0 ha. The highest estimates were for the bird that colonized the plot between 1995 and 1996. This bird apparently was unmated and appeared to move more than the paired birds. All of the other radio-tagged birds were mated, but even so, one individual had a territory of 15.9 ha (minimum convex polygon) to 26.3 ha (kernel). These birds were sampled less often than *F. colma*, so the estimates are more likely to be low. Based on the mean of high (26.3 ha) and low (5.9 ha) estimates from paired birds, or 16.1 ha, the 12 ha occupied by *F. analis* in 1995 represented 0.75 territories per 100 ha. This leads to a biomass estimate of 94 g per 100 ha. Had the spot-mapping been done in 1996, however, this estimate would have been increased to about 156 g per 100 ha by the addition of the bird that was not present in 1995.

Call notes from *F. colma* were among the most commonly heard vocalization at the site. After accounting for its higher density, however, *F. colma* called no more often than *F. analis*. Based on a density of 9.5 pairs per 100 ha, I recorded 13.1 calls per pair. In contrast, I recorded 14.7 calls per pair for *F. analis*. *Formicarius analis* clearly sang more often (21.3 songs per pair) than did *F. colma* (1.9 songs per pair). My observations of radio-tagged birds indicated that *F. analis* sang a few times each morning whereas *F. colma* did not, at least from June to August.

Both species were unresponsive to heterospecific playback, although they responded very aggressively to conspecific playback (Table 2). There was no significant difference between species in response to heterospecific vocalizations. Several individuals of both species approached to within 10 to 20 m in response to heterospecific playback, but most individuals simply milled around and exhibited no apparent agitation. Playing the *F. colma* tape during *F. analis* heterospecific trials often induced nearby *F. colma* to vocalize and approach the speaker. Thus, the heterospecific playback trial for *F. analis* sometimes included both visual and vocal stimulation by *F. colma*. This additional stimulation did not seem to affect the *F. analis* subjects.

In addition to examining a subject's response to a conspecific intruder, the conspecific trial enabled me to determine the position of a subject at the end of a heterospecific trial. In many cases, I could not follow the movements of silent subjects as they walked

TABLE 2. Response of anthruses to playback experiments (see Table 1 for scoring criteria). Interspecific differences in response to heterospecific playback tested with a Mann-Whitney *U*-test; intraspecific differences in response to heterospecific vs. conspecific playback tested with Wilcoxon signed-rank tests.

Species	Heterospecific playback ^a		Conspecific playback ^b	
	<i>n</i>	$\bar{x} \pm SE$	<i>n</i>	$\bar{x} \pm SE$
<i>Formicarius analis</i>	11	5.4 ± 0.3	11	8.2 ± 0.2
<i>Formicarius colma</i>	11	5.2 ± 0.4	11	8.3 ± 0.2

^a Heterospecific playback between species: $P = 0.46$.

^b Conspecific playback vs. heterospecific playback within species: *F. analis*, $P < 0.005$; *F. colma*, $P < 0.005$.

along the forest floor during heterospecific playbacks. A subject's immediate appearance at the start of a conspecific trial confirmed that it had not moved away gradually during the heterospecific trial. Both species were obviously agitated by the conspecific playback, but the typical response differed between species. *Formicarius colma* approached the speaker rapidly, in some cases flying, but vocalized little. *Formicarius analis* approached much more gradually, although it called and sang more.

Discussion.—*Formicarius colma* is considerably more common than *F. analis* in the forest north of Manaus. It has smaller territories and occupies a greater proportion of terra firme forest than *F. analis*. Although most of these results were from a single study plot, the relative abundance of the two species was similar to that derived from mist-net data at a series of continuous forest plots (Stouffer and Bierregaard 1995) and from spot-mapping in replicate continuous forest plots (J. A. Stratford and P. C. Stouffer unpubl. data).

My results provided no evidence that the difference in abundance between the species is related to interspecific interactions. First, the birds generally were ambivalent to heterospecific playback, although they responded very strongly to conspecific playback. Second, the two species did not avoid each other, at least based on their distribution in the 100-ha plot that I surveyed intensively. This also is supported by data from vocalization frequency; *Formicarius colma* called frequently, even when they were within a territory of *F. analis*. Presumably, this indicates that *F. analis*, the larger species, does not use interference competition to limit the abundance of *F. colma*.

These results differ dramatically from those reported for the same species in Peru, where *F. analis* is much more common and has smaller territories than *F. colma* (Terborgh et al. 1990, Robinson and Terborgh 1995). The strong asymmetry in response to heterospecific playback between the two species led Robinson and Terborgh to conclude that *F. analis* used its larger size to physically dominate *F. colma*, and that

this interference competition limited the density and vocalization frequency of *F. colma*.

Clearly, these species interact quite differently in Manaus compared with Peru. Why should this be the case? One factor that may be involved is the difference in productivity between the two sites. The area north of Manaus is thought to be among the least productive areas of Amazonia due to its pronounced dry season and poor soils (Gentry and Emmons 1987). Biomass of the two *Formicarius* species is about 970 g per 100 ha in Manaus (this study) compared with 2,000 g per 100 ha in Peru (Terborgh et al. 1990). Perhaps *F. analis* occupies sites of relatively higher productivity in Manaus, but most of the forest is suitable only for *F. colma*. The costs to *F. analis* to try to exclude *F. colma* from most of the forest may not exceed the benefits. If this were the case, however, then conflict between the two species would be expected where *F. analis* occurs. I have no evidence for this from playback experiments or observations of radio-tagged birds.

Additional work may show that these two species use different microhabitats or food resources in Manaus than in Peru, thus accounting for differences in their abundance and behavior. My observations of foraging behavior suggest that both species forage in the same manner in Manaus, i.e. by picking invertebrates out of leaf litter, but they may use different microhabitats or select different prey types. Terra firme forest north of Manaus has much more topographic variation than the floodplain forest where Robinson and Terborgh (1995) worked in Peru, so the two species may segregate by elevation or slope in Manaus. Based on spot-mapping and observations of radio-tagged birds, however, this does not appear to be the case. Both species are found on high and low areas, although both appear to avoid steep slopes, swamps, and large tree-falls. To understand the potential for competition at either site would require more detailed observations of habitat selection and foraging (e.g. Robinson 1981). At larger spatial scales, habitat selection of the two species probably differs between Manaus and Peru. Both species are rare in secondary growth around Manaus, although *F. colma* is proportionately more abundant (Borges 1995, Cohn-Haft et al. 1997, P. C. Stouffer and J. A. Stratford unpubl. data). In contrast, *F. analis* occurs more commonly in primary successional areas and lower, wetter areas in Peru (S. K. Robinson and K. Rosenberg pers. comm.)

Species turnover across adjacent habitats and seral stages is characteristic of tropical bird communities (Terborgh 1985, Robinson and Terborgh 1997). Interspecific aggression may be an important mechanism that drives species turnover, especially for closely related species occupying a successional or elevational gradient (Robinson and Terborgh 1995). This mechanism appears to have less relevance for congeners that occupy the same habitat, such as the two species of *Formicarius* in Manaus. In Peru, Robinson and Terborgh (1995) reported little or no heterospecific re-

sponse in three other genera of late-successional species. The forces regulating the distribution of the two *Formicarius* in Manaus are not clear, but they are not related to interspecific aggression.

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LITERATURE CITED

- BIERREGAARD, R. O., JR. 1988. Morphological data from understory birds in terra firme forest in the central Amazon basin. *Revista Brasileira de Biologia* 48:169–178.
- BIERREGAARD, R. O., JR., T. E. LOVEJOY, V. KAPO, A. A. DOS SANTOS, AND R. W. HUTCHINGS. 1992. The biological dynamics of tropical rainforest fragments. *BioScience* 42:859–866.
- BORGES, S. H. 1995. Comunidade de aves em dois tipos de vegetação secundária da Amazônia central. M.S. thesis, Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil.
- CATCHPOLE, C. K., AND B. LEISLER. 1986. Interspecific territorialism in Reed Warblers: A local effect revealed by playback experiments. *Animal Behaviour* 34:299–300.
- CODY, M. L. 1974. *Competition and the structure of bird communities*. Princeton University Press, Princeton, New Jersey.
- COHN-HAFT, M., A. WHITTAKER, AND P. C. STOUFFER. 1997. A second look at the "species-poor" central Amazon: The avifauna north of Manaus, Brazil. In press in *Studies in Neotropical ornithology honoring Ted Parker* (J. V. Remsen, Jr., Ed.). *Ornithological Monographs* No. 48.
- FEINSINGER, P. 1976. Organization of a tropical guild of nectarivorous birds. *Ecological Monographs* 46:257–291.
- GENTRY, A. H., AND L. H. EMMONS. 1987. Geographic variation in fertility, phenology, and composition of the understory of Neotropical forests. *Biotropica* 19:216–227.
- KENWARD, R. E. 1990. *RANGES IV: Software for analysing animal location data*. Institute of Terrestrial Ecology, Cambridge, United Kingdom.
- LOVEJOY, T. E., AND R. O. BIERREGAARD, JR. 1990. Central Amazonian forests and the Minimum Critical Size of Ecosystems Project. Pages 60–71 in *Four Neotropical rainforests* (A. H. Gentry, Ed.). Yale University Press, New Haven, Connecticut.
- MURRAY, B. G., JR. 1971. The ecological consequences of interspecific territorial behavior in birds. *Ecology* 52:414–423.
- MURRAY, B. G., JR. 1976. A critique of interspecific territoriality and character convergence. *Condor* 78:518–525.
- MURRAY, B. G., JR. 1981. The origins of adaptive interspecific territorialism. *Biological Reviews of the Cambridge Philosophical Society* 56:1–22.
- ORIAN, G. H., AND M. F. WILLSON. 1964. Interspecific territories of birds. *Ecology* 45:736–745.
- PRESCOTT, D. R. C. 1987. Territorial responses to song playback in allopatric and sympatric populations of Alder (*Empidonax alnorum*) and Willow (*E. trailii*) flycatchers. *Wilson Bulletin* 99:611–619.
- REMSEN, J. V., JR., AND D. A. GOOD. 1996. Misuse of data from mist-net captures to assess relative abundance in bird populations. *Auk* 113:381–398.
- RICE, J. 1978. Ecological relationships of two interspecifically territorial vireos. *Ecology* 59:526–538.
- RIDGELY, R. S., AND G. TUDOR. 1994. *The birds of South America, vol. II. The suboscine passerines*. University of Texas Press, Austin.
- ROBINSON, S. K. 1981. Ecological relations and social interactions of Philadelphia and Red-eyed vireos. *Condor* 83:16–26.
- ROBINSON, S. K., AND J. TERBORGH. 1995. Interspecific aggression and habitat selection by Amazonian birds. *Journal of Animal Ecology* 64:1–11.
- ROBINSON, S. K., AND J. TERBORGH. 1997. Bird community dynamics along primary successional gradients of an Amazonian whitewater river. In press in *Studies in Neotropical ornithology honoring Ted Parker* (J. V. Remsen, Jr., Ed.). *Ornithological Monographs* No. 48.
- STOUFFER, P. C., AND R. O. BIERREGAARD, JR. 1995. Use of Amazonian forest fragments by understory insectivorous birds. *Ecology* 76:2429–2445.
- TERBORGH, J. 1985. Habitat selection in Amazonian birds. Pages 311–338 in *Habitat selection in birds* (M. L. Cody, Ed.). Academic Press, New York.
- TERBORGH, J., S. K. ROBINSON, T. A. PARKER, III, C. A. MUNN, AND N. PIERPONT. 1990. Structure and organization of an Amazonian forest bird community. *Ecological Monographs* 60:213–238.
- WHITE, G. C., AND R. A. GARROTT. 1990. *Analysis of wildlife radio-tracking data*. Academic Press, San Diego.
- WORTON, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* 70:164–168.

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Influence of Weather on Breeding Success of Peregrine Falcons in the Arctic

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Many studies have examined the effects of weather on avian breeding success (e.g. Ojanen 1979; Wingfield 1984, 1988; Peach et al. 1991; Clarke and Johnson 1992; Hendricks and Norment 1992; Aebischer 1993; Sasvari and Hegyi 1993), but few studies have dealt specifically with raptors (e.g. Ridpath and Brooker 1985; Mearns and Newton 1988; Olsen and Olsen 1988, 1989a,b; 1992; Pietiainen 1989; Norriss 1995; Steenhof et al. 1997). Similarly, breeding success of Peregrine Falcons (*Falco peregrinus*) has been studied throughout their range (see Hickey 1969, Cade et al. 1988), but only two studies have evaluated the effects of weather on breeding success (Mearns and Newton 1988, Olsen and Olsen 1989b).

We gathered data on 310 territorial pairs of Peregrine Falcons (*Falco peregrinus*) over 13 breeding seasons to explore the relationship between breeding success and weather. Specifically, we examined annual variability in breeding success and the extent to which breeding success varies with weather. We also examined weather and breeding phenology, as this relationship affected breeding success. The two previous studies of weather and breeding success in Peregrine Falcons (see above) took place in relatively benign climates. In contrast, the climate at our study area in subarctic Canada ranks among the coldest and harshest within the species' breeding range.

Study area and methods.—The study area surrounds the Inuit hamlet of Rankin Inlet (62°49'N, 92°05'W) on the northwest coast of Hudson Bay in the Northwest Territories. The 450-km² study area was established in 1982. The climate at Rankin Inlet is characterized by short, cool summers (July mean temperature 10°C) and long, cold winters. Strong winds are common, and summer storms usually start after the first week of August. The Inlet freezes completely in November and does not break up again until July. Snow cover lasts from late September to early June. The habitat is flat, treeless tundra interspersed with rocky outcrops of the Canadian Shield. These rocky outcrops have been shaped by glacial action to form a series of southwest-facing cliffs. The ledges on these cliffs provide most of the nesting habitat. Nests

may be on oceanic islands, the coast, or inland. Eggs are laid in bowls scraped in the soil, or in old stick nests of Rough-legged Hawks (*Buteo lagopus*). The study population is migratory. Peregrine Falcons arrive on the study area in mid- to late May and lay eggs in the first week of June. The young fledge in mid-August and depart for the tropical Americas by late September. See Court et al. (1988a,b; 1989), Bradley and Oliphant (1991), and Johnstone et al. (1997) for additional details of the study population.

Data were collected from 1982 to 1994. The study area was thoroughly searched in mid-May each year. Most nesting sites were associated with an obvious growth of the lichen *Xanthoria elegans*, and an observer's approach to a territory usually elicited a defensive response from the resident pair. The flat, treeless topography made suitable cliffs easy to find such that more than 95% of the pairs were found prior to egg laying. Single birds on territories were not counted (and were quite rare). Nonlaying pairs were counted as territorial pairs if they were seen more than once and responded defensively to the observer. Nest visits during laying and hatching provided dates for the first egg laid and the first chick hatched. If the first-egg date was missed, it was estimated by subtracting the incubation period ($\bar{x} = 36.23 \pm \text{SD of } 2.29 \text{ days, } n = 44$) from the hatching date of the first chick. Each nest was monitored until fledging or nest failure. By continuously monitoring all nests, we avoided biases inherent in studies based on one or two surveys per year (Mayfield 1975, Steenhof and Kochert 1982).

Clutch sizes were based on territorial pairs so that proportion of pairs to lay and number of eggs laid could be incorporated into a single parameter. Egg mortality was calculated as clutch size minus the number of eggs to hatch. Sample size equalled number of laying pairs. Chick mortality was calculated as the brood size at hatching minus the brood size at fledging. Sample size equalled number of hatching pairs. Chicks were considered "fledged" at 25 days of age, even though the actual age at fledging was 35 to 40 days (see Steenhof and Kochert 1982:887). Chicks older than 25 days often wandered from the nest area and became difficult to locate.

Annual breeding phenology was established

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