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WINTER BEHAVIOR AND ECOLOGY OF THE ALDER FLYCATCHER (*EMPIDONAX ALNORUM*) IN PERU

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Resumen. – Comportamiento y ecología del Trapamosca Aliso *(Empidonax alnorum)* en Perú durante el invierno. – Se estudió la ecología y el comportamiento del Trapamosca Aliso *(Empidonax alnorum)* a lo largo del Manu, un río meandro de agua blanca en el Parque Nacional del Manu, Madre de Díos, Perú, durante Octubre y Noviembre, 1993–1997. Durante este período, las aves ocupaban territorios en hábitats en sucesión primaria en playas de creciente. Se encontraban mas comúnmente en vegetación mixta de *Tessaria integrifolia* (Asteraceae) y *Gynerium sagittatum* (Gramineaceae), alternada con áreas de arena desnuda. La característica más importante del hábitat era la irregularidad del dosel, la cual resultaba en aberturas suficientemente grandes en la vegetación que facilitaban la captura de insectos en vuelo. La ingestión de insectos comprendía el 96% de la dieta de estas aves; 91% de los insectos eran capturados en vuelo, 6% en vuelos cortos desde la percha y 3% en vuelo sostenido (como el de los colibríes). La ingestión de frutas constituía el 4% de la dieta. El tamaño de los territorios variaba entre 0,04 ha y 0,25 ha. De los nueve territorios que se observaban de cerca, seis estaban ocupados por dos individuos, dos por un individuo, y uno por tres individuos. En cada grupo había un individuo dominante, quien era el principal responsable de la defensa del territorio; las demás aves estaban asociadas a ese individuo. Las vocalizaciones incluían el canto de *fee-bee-o*, un canto de dos sílabas, y la nota del *pit*, también usada en las áreas de reproducción. Una serie de *pits* con rapidez creciente indicaba una interacción territorial. Durante los encuentros agresivos, las aves (1) permanecían en sus territorios mientras contestaban las llamadas o intercambiaban llamadas agitadas; (2) volaban hacia el límite de su territorio y se involucraban en un duelo vocal; o (3) el individuo dominante perseguía a los intrusos hasta que el último saliera del territorio. Las persecuciones eran más comunes cuando una ola de aves, no pertenecientes al grupo, entraba al área. Es muy probable que las aves dominantes, las cuales cantaban cantos enteros y defendían sus territorios con energía, fueran machos adultos. Los machos inmaduros no cantaban los cantos enteros, y no se sabe si las hembras cantan en la naturaleza. Probablemente, los individuos asociados eran machos inmaduros o hembras.

Abstract. – The winter ecology and behavior of Alder Flycatchers (*Empidonax alnorum*) were studied along the Manu, a white-water meander river in Manu National Park, Madre de Dios, Perú during October and November, 1993 to 1997. The birds occupied territories in primary-succession habitats on growing point bars. They were most common in mixed stands of *Tessaria integrifolia* (Asteraceae) and *Gynerium sagittatum* (Gramineaceae) interspersed with bare sand areas. The uneven height of the *Tessaria* canopy, which resulted in openings in the vegetation large enough for the birds to flycatch, was an important habitat feature. Birds obtained insects, which formed about 96% of the diet, by aerial hawking (91%), perch gleaning (6%), and hover gleaning (3%). They also fed on fruit. Territory sizes ranged from 0.04 to 0.25 ha. Of nine territories that we observed closely, six were occupied by two birds each, two by one bird each, and one by three birds. Every territory had one dominant individual who was primarily responsible for territory defense; the other birds were associates. Vocalizations given included the *fee-bee-o* song, a two-syllable song, and the *pit* note, which are also given on the breeding grounds. A series of *pits* given increasingly rapidly signaled a territorial interaction. In aggressive encounters, the birds (1) interacted vocally, remaining on their territories and counter calling or exchanging agitated calls; (2) moved toward a common territorial boundary and engaged in a vocal duel; or (3) the dominant chased intruders out of the territory. Chases were most common when a wave of new birds entered the area. Dominant birds, which sang the full song, were probably adult males. Immature males do not sing a full song, and females are not known to sing in nature. Associate individuals were likely females or young males. *Accepted 31 October 2006.*

Key words: Aerial hawking, Alder Flycatcher, *Empidonax alnorum*, Nearctic migrant, Perú, winter territory.

INTRODUCTION

Because of concerns about potentially negative population trends among species of Neotropical migrant birds, efforts are being made to assess the status and vulnerability of species and, if necessary, to develop strategies for their protection or management. To be effective, the latter plans must consider year-round biology and threats. This is often difficult because information about the biology of migrants during migration and on their wintering grounds is scarce (Poole & Gill 1992–2002). The Alder Flycatcher (*Empidonax alnorum*) is one of the species for which migratory and winter behavior and ecology are poorly known (Lowther 1999). In part this reflects a relatively recent recognition that the two song types of what was formerly Traill's Flycatcher represent separate species, the Willow (*E. traillii, fitz-bew* song type) and Alder (*fee-bee-o* song type) flycatchers (Stein 1958, 1963; American Ornithologists' Union 1973). Because in some areas these species occupy the same breeding, migration, and wintering ranges, accounts of the Traill's Flycatcher published prior to 1973 cannot be assigned to either component species unless investigators reported the song types of individual birds or worked in areas where only a single song type is known.

Alder Flycatchers winter on the eastern slopes of the Andes and into the adjacent lowlands from central Colombia south to northwestern Argentina (Ridgely & Tudor 1994, Lowther 1999). They occupy shrubby clearings, open woodlands, dense brush, and secondary succession, especially adjacent to water, as well as primary-succession habitats along the shores of floodplain rivers (Gorski 1971, Fitzpatrick 1980b, Ridgely & Tudor 1994, Lowther 1999, Nishida & Whitfield 2005, this study). I studied the early winter ecology and behavior of Alder Flycatchers in southeastern Peru between 1993 and 1997. I present the results of that study with comments about the vulnerability of the species to human-generated threats.

METHODS

The study was carried out along the Manu, a white-water meander river in Manu National Park, Madre de Dios, Perú. The principal observation sites were in primary-succession habitats on two river beaches known locally as Playa 104 (11°53'30"S, 71°23'52"W, elev. c. 331 m; Google Earth 2005), across the river from the Cocha Cashu Biological Station, and Playa 99 (11°54'36"S, 71°21'3"W, elev. c. 333 m), about 6.25 km ESE. Because the beaches increase in size each year and succession of the vegetation continues, these coordinates likely no longer designate habitats used by the birds. Vegetation in the early successional areas does not form a closed canopy and insolation is high, so habitats can be quite hot. During October and November, we recorded maximum daily shade temperatures from 34.5° to 37.8°C and minimum temperatures of 18.5° to 22.5°C. Rainfall at the Cocha Cashu Station for 1993 to 1997 averaged 254 mm in October (N = 5 yrs) and 244 mm in November (N = 4 yrs). The transition from the dry to the rainy season occurs over a period of a month or two in September–November. During that period, the beaches and *Tessaria* habitats are intermittently flooded with up to a meter or more of water. Once the rainy season begins, flooding is more frequent and persists for longer periods.

My assistants and I captured birds in vegetated sites along the length of each beach. We periodically used song playbacks of Alder Flycatcher vocalizations obtained from the Macaulay Library, Cornell University Laboratory of Ornithology, to lure birds into mist nets. We recorded a few vocalizations with a Sony Walkman and a Sennheiser directional microphone and analyzed them with Raven 1.2.1 and Signal 4.0 for Windows. We marked captured individuals with numbered metal bands and unique combinations of two colored, plastic tarsal bands. We weighed each bird, measured wing chord and tail length, and where possible, "skulled" the bird to determine age (Pyle 1997). We did not attempt to measure the lengths of individual primaries because of the difficulty of maintaining a uniform curvature of the wing when holding a live bird. We also examined the plumage for molt and wear, as a clue to age, and for staining by food or fecal material, and examined feces deposited by netted birds. In 1993, I laparotomized 10 birds in an attempt to sex them. Because the gonads were either fully regressed or undeveloped, only a few could be sexed with confidence. A few birds fell outside the zone of overlap in wing and tail measurements of males and females and were designated as the appropriate sex (Stein 1963). In 1996 and 1997 I collected a capillary tube of blood from each netted individual and stored it in 2ml of 70% ethanol. The samples were sexed genetically by PE Zoogen.

We observed Alder Flycatchers for a total of 385 h during 70 days in October and November, 1993 to 1997. Observations were concentrated at 2 territories in 1993 (103 h), 4 in 1994 (154), and 3 in 1995 (82). We observed birds with binoculars from 15 to 30 min after first light (05:30–06:00), generally until mid-morning. In two observation periods between 15:00 and 17:00, we detected only a single bird.

We flagged "favorite perch trees" (FPT) used repeatedly for perching, preening, feeding, calling, and intraspecific interactions, and noted their heights, DBHs, and species identifications. We also recorded perch heights. Marked locations were mapped and used along with behavioral observations to define territory boundaries and determine habitat use. The area of each territory (minimum convex polygon) was estimated using Design Cad Express version 12. We recorded types of vocalizations, the identity of the individual vocalizing, time of day, and circumstances under which a call or song was given. When possible, we noted perch heights both before and after a feeding sally, method of prey capture, direction and distance of feeding maneuvers, and food type (insect or fruit). Terminologies for methods of prey capture and foraging modes follow Fitzpatrick (1980a). We described intraspecific interactions in detail, noting the location, birds involved, vocalizations, and time of day.

RESULTS

Arrival

We first detected Alder Flycatchers, which we identified based on their vocalizations, in mid-October (cf. Fitzpatrick 1980b). Because the birds are extremely selective about the beaches on which they settle, it was difficult to determine first-arrival dates. The birds never settled on some beaches that we visited regularly but were present on other beaches the first time we checked. The earliest we detected a bird in the study area was on Playa

FIG. 1. Primary succession on point bars along the Manu River, Madre de Dios, Perú, showing three bands of *Tessaria integrefolia.* Arrows indicate zones of *Tessaria* as one moves away from the water: youngest, low growing shrublets nearest the open beach; middle zone of shrubby growth; and zone of trees. Invading caña brava is visible in the tree zone.

99 on 16 October 1996. In 1993, however, birds were first located on 19 October on Playa 104, although we had searched for them on that beach using song playback beginning on 6 October. The first birds to arrive set up territories in appropriate habitat along the narrow strip of early successional vegetation adjacent to the beach. At irregular intervals (7–14 days), waves of additional birds (estimated at 3–10 individuals) arrived at a beach, stayed one or two days, and disappeared. The latest date that we observed a wave of birds was 11 November.

We banded 55 individuals between 1993 and 1997, 12 females, 19 males, and 24 of indeterminate sex. Only 5 of the banded individuals occupied territories that we observed. No individual was seen in more than one year. Twelve birds we examined had fully pneumatized skulls. Six others had small skull windows posterodorsally, which suggests that they were birds of the year (Pyle 1997). Fourteen of the birds had new, unworn plumage, in excellent condition. Two birds were in heavy molt, including the flight feathers, and five were in the last stages of molt. In eight birds the plumage was obviously worn, especially the flight feathers.

Habitat use

Primary-succession habitats along whitewater meander rivers are found on developing beaches, which extend into the river. The growth of the beach and its colonization by vegetation are complex dynamic processes which are described in Salo *et al.* (1986), Kalliola *et al.* (1987, 1988), and Puhakka *et al.* (1993). The initial and most common coloniz-

FIG. 2. Irregular primary succession on point bars along the Manu River, Madre de Dios, Perú, showing scattered individuals and clumps of *Tessaria integrefolia* and caña brava interspersed with open areas of bare sand.

ing species in the Manu is *Tessaria integrifolia* (Asteraceae), known locally as "pájaro bobo;" balsa (*Ochroma pyramidale,* Malvaceae) and willow (*Salix humboldtiana,* Salicaceae) may also be present. *Tessaria* begins as scattered clumps of low vegetation on the open sand and silt. Over the next several seasons, these fast growing plants form a dense shrubby layer and then a forest of successively larger trees (up to 16-m tall and 13-cm DBH). Because new areas of beach are colonized seasonally, each levee tends to be occupied by a dense, even-aged stand of *Tessaria* trees of more or less uniform height. Thus, by walking perpendicular to the point bar and away from the water, one crosses clearly evident zones of successively older and larger trees (Fig. 1).

Tessaria live from 8 to 15 years before senescing and dying (Lossada *et al.* 1969, as cited in Domínguez Faura 1995; Kalliola *et al.* 1988). When the *Tessaria* trees are 2 to 3 m tall, the stands are invaded by caña brava (*Gynerium sagittatum,* Gramineaceae), which grows up among the *Tessaria.* Gradually, other species, such as *Cecropia membranaceae* (Cecropiaceae) and *Guarea guidonea* (Meliaceae), become dominant (Foster 1990). They overtop and shade out the *Tessaria* and caña, and the understory becomes more open. In the next phase of succession *Ficus insipida* (Moraceae) and *Cedrela odorada* (Meliaceae) become dominant.

Although the successively older zones of *Tessaria* may be clearly distinguishable (Fig. 1), many factors can influence the establishment, growth, and persistence of the plants. Consequently, the vegetation is not always as regular or uniformly distributed as described above (Salo *et al.* 1986; this study). On some beaches the density and heights of *Tessaria* trees vary

TABLE 1. Characteristics of non-feeding perches used by Alder Flycatchers (*Empidonax alnorum*) wintering along the Manu River, Manu National Park, Madre de Dios, Perú.

Characteristics	N[a]	Range	Mean ± SE	CV
Perch height (m)	251	0.5–13.0	5.0 ± 0.15	46
Tree height (m)	295	1.8–16.0	7.7 ± 0.17	38
Disance below tree top (m)	168	0.0–14.0	2.1 ± 0.14	88

[a]Samples do not include perches used for feeding.

considerably. The trees may form irregular patches or stringers (narrow strips of trees; Lynn *et al.* 2003) of varying size and length. Both clumps and stringers are commonly separated by patches of bare sand from a few to tens of meters across, as well as interspersed with monospecific stands of young caña or older *Tessaria* (Fig. 2).

We found Alder Flycatchers throughout the *Tessaria* zone, from the shrub (≥ 1 m tall) stage at the edge of the beach, through mixed *Tessaria*/caña stands, and into areas of trees beginning to senesce. However, the birds were by far the most common in mixed stands of *Tessaria* and caña brava with plants of variable heights, especially those interspersed with patches of bare sand (Fig. 2) or bordering sandy, open backwaters. We heard or observed them occasionally in early successional forest from which nearly all *Tessaria* trees and caña stems had disappeared, and rarely into the early successional forest stage dominated by *Ficus insipida* and *Cedrela odorata*. We almost never observed them in dense stands of *Tessaria* of uniform height.

Alder Flycatchers nearly always perched in *Tessaria*, which was the most common plant in the habitat. Occasionally a bird perched on a horizontal caña leaf (N = 9 observations) at heights ≤ 2 m. Birds perched in five species of non-*Tessaria* trees only seven times, and one bird used a dead snag three times. Branches of *Tessaria* trees are relatively horizontal, forming a wide angle (60º–90º) with the trunk above. As the trees grow, the lower branches die and slough. Thus, the birds perch higher above the ground in taller trees, nearly always using live branches, whose leaves are concentrated distally. The heights of *Tessaria* trees used by the birds and the heights of their (non-feeding) perches above the ground covered a wide range (Table 1).

Territoriality

Birds established territories in the *Tessaria* zone, from the shrub stage at the edge of the beach through mixed *Tessaria*/caña stands, although territories occasionally extended into areas where the trees were beginning to senesce. The birds we observed did not defend territories in the *Ficus*-*Cedrela* zone. Because the zone of appropriate habitat was relatively narrow, territories usually formed a single row along the length of the beach, although in a few places, they were two deep. We identified two territories on Playa 104 in 1993, none in 1994 and 1995, two in 1996, and at least two (more may have been present) in 1997. At least six territories were present on Playa 99 in 1994, four in 1995, and none in 1996 and 1997. The three territories on Playa 99 in 1995 were located in approximately the same areas as three of the territories in 1994, but were much smaller (Fig 3; Table 2). The 9 territories we observed closely ranged in size from 0.04 to 0.25 ha. Six were occupied by two birds each, two by

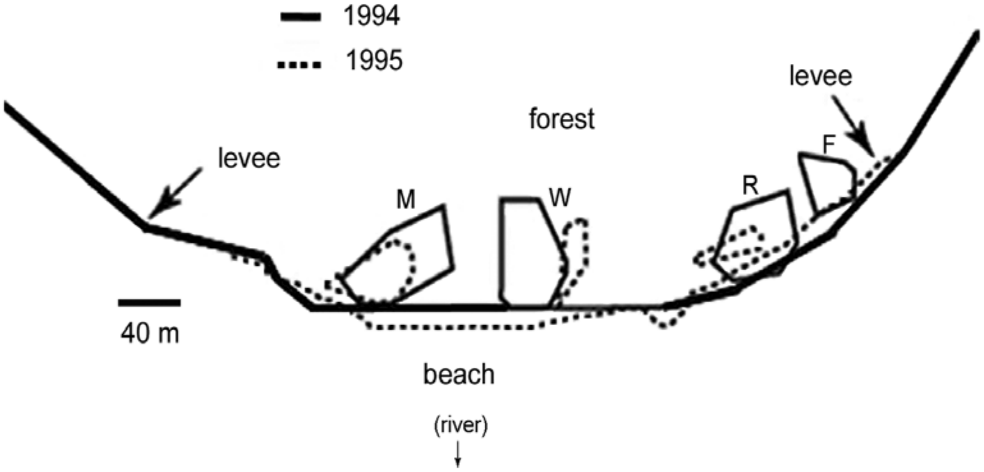

FIG. 3. Territories (polygons) of Alder Flycatchers (*Empidonax alnorum*) on Playa 99 on the Manu River, Madre de Dios, Perú in 1994 (solid line; 4 territories) and 1995 (dashed line; 3 territories). Letters correspond to territory designations in Table 2. The levee represents the boundary between the beach and the first levee with shrubby *Tessaria integrefolia* in 1994 (solid line) and 1995 (dashed line).

TABLE 2. Size and occupancy of winter territories of Alder Flycatchers (*Empidonax alnorum*) along the Manu River, Manu National Park, Madre de Dios, Perú.

Territory	Area (ha)	No. birds	Area/bird (ha)
93-N	0.23	2	0.12
93-S	0.10	2	0.05
94-M	0.25	2	0.13
94-W	0.23	2	0.12
94-R	0.20	3	0.07
94-F	0.08	2	0.04
95-M	0.14	2	0.07
95-W	0.06	1	0.06
95-R	0.04	1	0.04
Mean ± SE	0.15 ± 0.03	1.9 ± 0.20	0.07 ± 0.01

one bird each, and one by three birds. The area per bird ranged from 0.04 to 0.12 ha. In all instances, the presence or absence of territories and territory size reflected the amount of appropriate habitat. Large territories included a greater range of *Tessaria* growth forms (e.g., shrubs, saplings, trees) and sizes, the trees and caña were more irregularly distributed, and the open spaces larger than in small territories. They were generally more open and more light reached the ground than in uniform stands of *Tessaria* trees (Fig. 2).

Every territory was occupied by a bird that I designated as the dominant individual, or territory owner. This bird patrolled the perimeter of the territory moving among FPTs that it used repeatedly. It called early in the morning, and sang the full *fee-bee-o* song vigorously, although infrequently. The dominant was also primarily responsible for defense of the territory (see "*Territorial behavior*," below). On three of the territories we observed, this individual was color banded; on another, it had an easily recognized plumage peculiarity. I termed the other bird(s) on a territory the "territory associate(s)." The

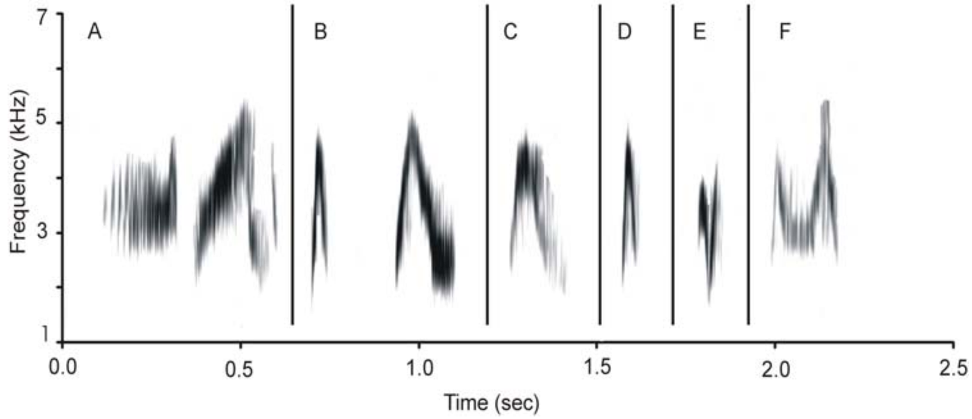

FIG. 4. Sound spectrograms of vocalizations made by Alder Flycatchers (*Empidonax alnorum*) on their wintering grounds along the Manu River, Madre de Dios Perú: (a) *fee-bee-o* song; (b) *pit-wee-weer* call; (c) *zwee-oo* call note; (d) *pit* call note; (e) *churr* call note; (f) double-peak call note.

dominants did not challenge these birds, which, in general, were much less active although they occasionally engaged in aggressive squabbles with intruders. Interestingly, the associate tended to stay close to the dominant individual. The birds often perched together in the same *Tessaria* tree, always with the dominant 1.0 to 1.5 m above the associate. The associate occasionally moved with the dominant, following it around the perimeter of the territory as it patrolled. Two of the associates were color banded.

Of nine birds that we identified as dominants, seven had worn plumage, especially the flight feathers; one was molting both body and flight feathers; and one had plumage that was in good condition. In contrast, the plumages of most birds identified as associates looked new, with no noticeable wear on the flight feathers. The plumage differences facilitated distinguishing between even unbanded occupants on a territory. I do not know the sex of any of the banded birds on the territories, although one had a wing length of 72 mm, which suggests that it was an adult male. One of the birds had a pneumatized skull; another had small skull windows. Those two birds behaved as dominant and associate individuals, respectively

Vocalizations

The birds sang and called regularly beginning between 05:30 and 05:45, about 30 min after first light. Although any call might be heard, more than 80% of the vocalizations before 06:00 were *fee-bee-o* songs and *pit* calls. The frequency of vocalizations diminished significantly after about 08:00, and the birds became less active and less conspicuous. After 09:00, we heard only an occasional call and no songs. The calls are described phonetically, below. The variants illustrate the difficulty of describing the vocalizations verbally but do not indicate that the vocalizations, themselves, varied significantly. Call names follow Lovell & Lein (2004).

Fee-bee-o. This vocalization (Fig. 4a) is the advertising song used by Alder Flycatchers to indicate their presence and define the perimeters of their winter territories. The birds often sang from FPTs, although individual singing bouts rarely lasted for more than 30 s or included more than a few songs; they sometimes sang while patrolling. One longer bout (3.5 min) was given by a recently arrived bird that may have been establishing its territory.

In addition to the 3-syllable song, we heard a variety of 2-syllable songs. Some of them had a harsh, raspy tone; others were smooth and more melodic. The second note of these vocalizations has an "ee" sound (e.g., *fee-bee, pee-we, shu-ee, wee-bee,* etc.). The second syllables were sometimes given alone, and when the birds were agitated**,** often sounded like a *wheeze*. These vocalizations likely represent the same two-note song described by other authors as consisting of the first two notes of the *fee-bee-o*, with the third syllable absent or, more likely, too soft to hear (e.g., Zink & Fall 1981, Whitney & Kaufman 1986, Lowther 1999, M. R. Lein pers. com.).

Birds often preened or fed between songs. Dominant birds on adjacent territories sometimes sang antiphonally at a moderate rate and not particularly forcefully. They also sang the f*ee-bee-o* and two-note songs during aggressive interactions (see "*Territory defense*," below).

Whee (or *wheet*). This call (Fig. 4f) is the "double peak" call described by Lovell and Lein (2004: fig. 2B). In the field, it can sometimes be confused with the smoother and more melodic two-note *fee-bee* call. The call was given during aggressive encounters.

Zwee-oo. In this two-syllable call (Fig. 4c), the second note has an "oo" sound (e.g., *pee-oo, shu-u, tu-woo; phew-u,* etc.). The call, which is also given on the breeding grounds (Stein 1963, Lovell & Lein 2004), was given during aggressive interactions.

Pit. The most commonly given call was the *pit*, also variously described as a *chup, chuck, chip*, and *peep* (Fig. 4d). All the birds we observed gave this call frequently, either alone, or intermixed with any of the other calls. When given alone, call bouts lasted from a few seconds to 3.5 min. Lone birds gave this call when perched or moving around, as if to indicate their presence and location to other birds on their own or adjacent territories. Two birds also gave it in an uncoordinated fashion when they perched close by on a single territory, or antiphonally when on the same or adjacent territories. During intraspecific aggressive interactions, the call was loud and forceful, and the rate of calling increased noticeably.

Churr. These calls were given once or many at a time in rapid succession (Fig. 4e). In the latter instance, we variously described the call as a *warble*, *squabble*, or *trill*. Rapid series of calls often followed agitated bouts of countersinging of the *fee-bee-o* song, chases, or other aggressive interactions.

Pit-wee-weer (*chuck-wee-weer, pit-er; chuck-e-ah, pit-we-ars; pit-we-ear*). The cadence of this call evokes the *quick-three-beer* song of the Olive-sided Flycatcher (*Contopus cooperi*) but has a raspy rather than a melodic whistling sound (Fig. 4b). It was given by a lone bird patrolling its territory perimeter or during territorial interactions. As a bird became increasingly agitated, the *we-weer* gave way to *whee-er*, *wheer*, and *wheeere*, with the syllables running together and the *pit* note omitted. This call-song sequence is often given on the breeding grounds by birds that are aggressively aroused (M. R. Lein pers. com.).

Miscellaneous other calls were heard occasionally, but in the absence of recordings it wasn't possible to reconcile them with calls described by other researchers.

Territorial behavior

Dominants occupying territories patrolled them regularly, circumscribing the perimeter by flying among FPTs in a regular sequence. Birds sometimes patrolled in silence, called or sang occasionally by themselves, counter-called *pit* notes with an associate on the territory, or counter-called *pits* or countersang *fee-bee-os* with birds on adjacent territories. During routine patrols, birds moved around the perimeter at a moderate pace, occasionally stopping to preen or feed. Calls of birds interacting with non-associate conspecifics were louder, more frequent, and harsher; in addition the birds moved more quickly among perches and did not engage in other activities. Patrolling birds usually perched between 5 and 6 m above the ground (except in areas consisting only of low shrubs) regardless of tree heights. When especially excited, however, they often moved among perches within 0.5 m of the ground, regardless of vegetation height. Patrolling birds that we were able to identify were always dominant individuals. Once, however, as a dominant bird patrolled its territory perimeter using perches 5 to 6 m up, a second bird followed it several meters behind, using perches 1.5 to 2 m above ground. Usually, the associate on a territory sat quietly or gave soft *pits* from a FPT.

A series of *pits* given with increasing frequency–up to 24/min–signaled the onset of a territorial interaction. At the lowest levels of aggression, the birds interacted vocally, remaining on their own territories and usually not appearing to be in visual contact. The birds exchanged a series of *pits, zwee-oos*, 2-note songs, or other calls, with no recognizable pattern. Most commonly, however, they countercalled or countersang for from 30 to 120 sec, exchanging rapid series of often, harsh *fee-bee-os* (7 encounters); *pits,* which often were followed by *squabbles* or *churrs* (5); or a mixture of vocalizations (*pits*, *fee-bee-os*, *pee-oos, wheezes*, *wheets*, 6). One bird did a wing-flick (Stein 1963). Usually, an exchange simply ended, but occasionally one bird continued singing from an exposed perch after the other stopped.

Sometimes, after a series of rapid *pits* and harsh *squabbles* or *churrs*, the birds moved toward a common territorial boundary and into visual contact. They engaged in a vocal duel countersinging loud, forceful *fee-bee-os*, or giving harsh call notes such as *pits*, *pee-oos*, and *churrs.* The birds hopped around on their perches, closely watching their opponents. One bird tail-flashed (Stein 1963). After 15 to 30 sec of interaction, the birds returned to their respective territories continuing to *pit* quietly.

Interactions of the greatest intensity involved chases. Again, interactions were signaled by *pits* followed by *squabbles,* and once, we heard bill snapping. The dominant bird on the territory flew rapidly and silently after the trespasser but stopped at the territory boundary, whereas the intruder kept on flying. The owner then retired to an exposed perch where it gave a long series of harsh, loud *fee-be-oos*, *pits*, *wee oos, wee ars, tee was*, c*huck wee weers,* or any combination thereof. Chases were most common when a wave of new birds entered the area and probably were directed at new arrivals rather than birds from adjacent territories.

Nearly all interactions involved dominant birds. However, in three instances, two birds on adjacent territories countercalled with a rapid series of very loud *pits* while a third bird on one of the territories sang *fee-bee-o* songs. In another instance, two birds on adjacent territories countersang, while a third bird on one of the territories gave soft *pits.*

Feeding

We recorded 185 bouts of feeding primarily by the 17 birds on territories. In bouts in which a food item was visible, 78 were insects and seven were fruits. Insects were taken most commonly by aerial hawking (162, or 91% of observations) in which a bird flies from its perch directly at a flying insect and snatches it from the air. An Alder Flycatcher usually flew slightly upward, intercepting the insect from 0.5 to 1.0 m from the perch. It then flew downward to a level below the original perch and swung upward again to perch. It turned, describing a loop trajectory, and reoccupied the original perch 48% (N = 42) of the time. It continued to a new, forward perch, describing an s-shaped trajectory, 52% (N = 46) of the time. The average perch heights before (3.5 m) and after (3.8m) aerial feeding, when the birds moved to a new perch, did not differ significantly (t = -0.50292, *P* = 0.62, 38 df) from each other or from the average perch height (3.3 m) when the birds returned to the same perch (t = 0.33204, *P* = 0.74, 81 df.; t = -0.96369, *P* = 0.34, 59 df). The birds also fed by perch-gleaning (N = 10, 6% of observations), in which a perched bird removed an insect from the undersurface of a nearby leaf, and hover-gleaning (N = 6, 3%). The birds foraged most commonly from perches in *Tessaria* (N = 119), followed by caña brava (N = 9) and *Ficus insipida* (N = 2). The heights of the plants from which the birds foraged was highly variable, ranging from 2 to14 m (mean = 5.9 m, SD = 2.3, N = 82), with perches located an average of 1.9 m (range = 0.1–5.5 m, SD = 1.0, N = 78) below the top of the tree. Birds generally did not forage for several insects in rapid succession, and each feeding bout lasted only few seconds.

Bouts of fruit-feeding were longer. One bird foraged for more than 8 min, another for more than 10 min on fruits of a *Cissus* sp. (Vitaceae) vine twining through a *Tessaria* tree. They perched on the tree or vine and peered around looking for ripe fruit. Birds plucked fruits and swallowed them whole, similar to the way in which they perch-gleaned insects from foliage. One bird snatched a fruit (*Struthanthus* sp., Loranthaceae) on the wing. Nineteen netted birds deposited fecal material; 16 of those samples contained fruit remains (*Cissus* sp., *Struthanthus* sp., but most unidentified), one contained insect remains, and two contained remains of both fruit and insects. The feathers around the vent and on the lower abdomen of four additional birds were stained with purple juice from an unknown fruit species.

DISCUSSION

The territorial and vocal behavior of Alder Flycatchers on the wintering grounds closely resembles that of the birds during the breeding season, although we only once observed any visible manipulation of the wing, tail, crest, or breast feathers (Stein 1958, 1963; Gorski 1969, Lowther 1999). In addition, structural aspects of the vegetation appear similar in both places, at least superficially. *Tessaria integrefolia* has been described as willow-like (Terborgh *et al.* 1984), and one Spanish common name for the species is "aliso del río," or river alder. The habitat was also essentially the same as the streamside habitats used by the Willow Flycatchers in Central America (Lynn *et al.* 2003) and by Alder and Willow flycatchers in Ecuador (Nishida & Whitfield 2005), where the birds were found predominantly in somewhat open areas of *Tessaria* and caña brava.

Feeding. The birds we observed foraged primarily by aerial hawking, as was also noted by Gorski (1969) on the breeding grounds. In contrast, Fitzpatrick (1980a), who observed winter birds at Cocha Cashu Biological Station, reported that they used primarily enclosed perch hawking and sally gleaning because of relatively small openings in the foliage and low light intensity. He noted, however, that aerial hawking increased when the birds entered larger openings or foraged at the edges of clearings. The differences in our observations may reflect differences in the habitats where we worked. Fitzpatrick reported that Alder Flycatchers occupied the "brushy new growth" of the primary succession and the "dense brush" at the edge of a lake and, presumably, he observed them feeding in those areas (Fitzpatrick 1980a, 1980b:74). We did not encounter birds at the lake edge, but they were regular inhabitants of the more open areas of the primary succession, where we made nearly all our observations. Those areas had sufficient space for aerial hawking and greater light availability, compared with the zones of dense, shrubby, even-aged stands of *Tessaria.* In fact, the most important feature of the habitat for the birds seemed to be openings among the *Tessaria* trees that allowed the birds to sally out to flycatch. Those openings reflected the uneven height of the canopy, the variable densities of trees and caña brava, and the presence of patches of bare sand. Barlow and McGillivray (1983) noted that the percent of hawks increased from 14% to 55% of all foraging moves when Alder Flycatchers on the breeding grounds occupied more varied vegetation. Our observations suggest that they do the same on the wintering grounds. Finally, we observed birds on territories, both residents and intruders, almost exclusively. Fitzpatrick did not indicate that the birds he observed were territorial, so they could have been floaters excluded by conspecifics from the more open areas of *Tessaria.*

Numerous species of Nearctic migrants (including Tyrannids) eat varying quantities of fruit during migration and winter (e.g., Beal 1912, Morton 1980, Rappole *et al.* 1983, Rappole 1995). Thirteen of the 15 species of *Empidonax* have been reported to do so, including all migrant species that breed in the United States and Canada (Beal 1912, Wetmore 1972, Rappole *et al.* 1983, Stiles & Skutch 1989, Koronkiewicz & Sogge 2000). It appears, nevertheless, that insects remain the predominate food in winter, particularly among territorial species (Rappole 1995).

Territoriality. At least some of the Alder Flycatchers were territorial on the wintering grounds, using vocalizations and agonistic behaviors comparable to those described for the breeding season (Stein 1958, 1963). The territories we encountered averaged only 0.15 ha (Table 2), smaller than the one (c. 0.2 ha) Gorski (1971) reported from eastern Peru, although those he described from scrubby areas along roads may have been smaller (Gorski 1969). In contrast, the breeding territories that Stein (1958) studied were nearly 10 times as large (mean = 1.9 ha, N = 3), although those studied by Gorski (1969) were not (mean = c. 0.2 ha, N = 12). The smaller size of the winter territories may reflect decreased energy demands in winter compared with those during breeding, or they may indicate that food availability is greater. Gorski (1969) noted, for example, that territory size increased toward the end of the breeding season when fledglings were present and the adults went farther to find food. Insect density is high in *Tessaria* habitats, which are among the richest in the Manu floodplain (J. W. Terborgh pers. comm.). Koronkiewicz (2002) reported differences of 67% to 70% (depending on the sex of the territory holders) in mean winter territory sizes of Willow Flycatchers at two localities in Costa Rica, which suggests flexible territory size depending on available resources. Alder Flycatchers may exhibit the same flexibility.

Various researchers have resighted and recaptured banded Willow and Alder flycatchers on the wintering grounds between years (Gorski 1969, 1971; Koronkiewicz & Sogge 2000, Koronkiewicz 2002, Nishida & Whitfield 2005). Site fidelity has also been reported for wintering Least (*Empidonax minimus,* Ely 1973, Ely *et al.* 1977), Acadian (*E. virescens,* Whitehead & Taylor 2002), and Yellow-bellied (*E. flaviventris*; Ely 1973, Ely *et al.* 1977, Rappole & Warner 1980) flycatchers. We did not record any of our banded birds between years. This difference may reflect the limited amount of appropriate habitat on any given beach and the likelihood of changes in the beach vegetation between years as well as the fragmented nature of suitable beach areas along the Manu River. Birds wintering in more extensive and stable patches of second growth and scrubby edge may be more likely to return to sites used in previous years.

It is likely that wintering Alder Flycatchers establish winter territories along meander rivers throughout the Amazon Basin. It may be, however, that only a portion of the population occupies territories, with the other birds moving about in small flocks. Thus, the waves of birds that periodically entered our study sites may have been newly arrived migrants (cf. Stiles & Skutch 1989) or wandering floaters so far unsuccessful in finding suitable habitat for territories. Floaters have been reported for Willow Flycatchers, which also defend winter territories (Koronkiewicz 2002).

The make up the territory occupants awaits confirmation. The dominant birds sang the full song and vigorously defended their territories. In addition, most of them had noticeably worn plumage. Both of these factors suggest that the territory owners were adult (second year [SY] or older) males (Whitney & Kaufman 1986, Pyle 1997). If the dominants were all SY or older males, it is tempting to assume that the associates were either females or young birds of either sex. With only one exception, associates did not sing the *fee-bee-o* song, but gave primarily *pit* calls. Kroodsma (1984) reported that hatching year (HY) males in an experimental laboratory study sang a song similar to the adult *fee-bee-o* soon after fledging, but that they did not vocalize in winter and did not sing a fully adult song until the spring of their second year. Likewise, female Alder Flycatchers are not known to sing in nature (Stein 1958, Seutin 1987), although Stein (1963) suggested that they may do so occasionally. Females do defend areas on the breeding grounds, but only within 5 m of the nest (Gorski 1969). Finally, the absence of noticeable wear on the feathers of most birds identified as associates suggests HY birds (Whitney & Kaufman 1986, Pyle 1997).

If associates are adult females and/or HY birds of either sex, it could mean that family groups migrate together. If they are females, it may indicate that pair bonds persist following reproduction or that new pair bonds are formed quickly on the wintering grounds, in which case the pair should migrate north together in the spring. It may also be that the winter territorial behavior of Alder Flycatchers is different in other, more extensive habitats, as well as in the presence of Willow Flycatchers. Both sexes of the latter species sing the advertising song and give call notes. They also defend mutually exclusive winter territories in Costa Rica (Koronkiewicz 2002, Seutin 2002) as do males and females of the Yellow-bellied and Least flycatchers in Mexico (Rappole & Warner 1980).

CONSERVATION STATUS

At present, Alder Flycatcher populations show no evidence of decline. Anecdotal reports suggest that the behaviorally dominant Willow Flycatcher may be expanding its breeding range northward, displacing the Alder Flycatcher, whose breeding range is shrinking (Stein 1963, Prescott 1987), but other workers question that conclusion (M. R. Lein pers. com.). Loss or degradation of riparian habitats on the wintering (and breeding) grounds could also influence population trends (Nishida & Whitfield 2005). Although the species may winter in shrubby clearings, open woodlands, and second-growth areas near water, primary successional habitats along meander rivers in the Amazon Basin are clearly important. Because these floodplain habitats are renewed each rainy season by silt deposition, they tend to be fertile and, therefore, potentially vulnerable to development for agriculture. In addition, plant species (particularly *Tessaria*) characteristic of the primary succession are fast-growing and produce fiber that is suitable for paper pulp (Lossada *et al.* 1969). So far, high transportation costs arising from impediments to river transport, towering mountains, and distances from markets have constrained the commercial development of these riverside habitats. However, new roads and more sophisticated types of transportation may lead to development and degradation of this important winter habitat. Because primary succession habitats constantly "migrate," however, it may be possible to develop land-use plans in which only the post-*Tessaria* successional stages are cleared for agriculture and only the zones of the tallest, most mature *Tessaria* are cut for paper pulp.

Preservation of the *Tessaria*/caña brava habitat is important not only for the Alder Flycatcher, but also for the more than 100 other species of birds (residents and nearctic migrants) reported to use it, seven of them exclusively (Terborgh *et al.*1984). With additional data on the dynamics of the vegetation and habitat use by these birds and other animals, it may be possible to design a development plan compatible with maintenance of the wildlife.

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