

## FORAGING BEHAVIOR OF TUFTED TIT-TYRANTS (*ANAIRETES PARULUS*) IN SEMIARID NORTHCENTRAL CHILE

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**ABSTRACT.**—We studied foraging behavior of Tufted Tit-Tyrants (*Anairetes parulus*) in Matorral (shrubland) habitat of northcentral Chile. This species is a generalist insectivore feeding in most shrubs of Matorral habitat at our study site, although they favored three of the dominant plant species. Their foraging is typical of small tyrannid flycatchers, using rapid perch gleans coupled with hover gleans and supplemented by flycatching. They use relatively long search periods (3–5 sec) followed by rapid gleans, which is typical for small tyrannids. Their active foraging ( $3.1 \pm 1.8$  prey attacks/min) coupled with a longer search time distinguishes them from parids or regulids of the Holarctic with which they often are compared. They generally forage singly or in pairs and aggressively defend what appears to be foraging territories in winter and summer. Densities of Tufted Tit-Tyrants at our study site were higher than reported in other studies from Chile and Argentina, presumably reflecting resource availability. Received 3 March 2008. Accepted 18 February 2009.

The *Anairetes* (Tit-Tyrant) flycatchers of South America inhabit dense scrublands and forested regions from southern Colombia to Patagonia; one species is endemic to the Juan Fernandez Islands (Ridgely and Tudor 1994). Six species are included in the genus (Ridgely and Tudor 1994, Roy et al. 1998) in the subfamily Elaeniinae, which is closely aligned with *Serpophaga* tyrannulets (Birdsley 2002). *Anairetes* have been termed “titlike tyrants” (Goodall et al. 1957) or “tit-tyrants” (de Schauensee 1966), reflecting behavioral and morphological similarity with Holarctic parids (chickadees and tits). Other authors have compared the foraging behavior of *Anairetes* to Holarctic regulids (kinglets) (Jaramillo 2003). The most widespread species of the genus is the Tufted Tit-Tyrant (*A. parulus*), which occupies diverse habitats including Andean pre-Puna scrub, desert scrub, Valdivian forest, and other shrublands. It occurs in most scrublands and forests in Chile below 2000 m (Jaramillo 2003). This species is insectivorous and its broad habitat, and latitudinal and altitudinal distributions suggest it is a habitat generalist. Their energetic style of foraging has been described as appearing to be “in constant motion, more so than most other gleaning tyrannids” (Smith 1971: 269). However, their foraging behavior and habitat preferences have not been quantified. Our objectives were to assess: (1) abundance, (2) foraging behavior, (3) prey-capture methods, and (4) plant associations of Tufted Tit-Tyrants in semi-arid Matorral (shrublands) in north-central Chile. We made

observations in summer and winter, and compared our results with predictions from Fitzpatrick’s (1981) models of search strategies in tyrant flycatchers.

### METHODS

We conducted our studies in the Quebrada de las Vacas, an interior valley in Parque Nacional Bosque de Fray Jorge (“Fray Jorge”). Fray Jorge comprises 9,959 ha on the coast of Chile’s IV Region, 400 km north of Santiago and 100 km south of La Serena (30° 41’ N, 71° 40’ W) (Fig. 1). The habitat is coastal steppe Matorral (Gajardo 1993), characterized by dense (50–60%) ground cover of drought-resistant shrubs (Gutiérrez et al. 1993). We focused our efforts in and around a long-term research station established to monitor ecological responses to abiotic influences (Meserve et al. 2003, Kelt et al. 2004). Avian inventories began with initial surveys in 2002 followed by quantitative studies of avian populations beginning in 2004. We visited our field site twice annually for this study and gathered foraging observations during three trips: 20–28 February 2002, 21–28 February 2004, and 28 July–10 August 2006. Observations were made by both authors. The avian study site is centered on the field station and comprises a series of eight transects spanning 6.5 km of Matorral habitat in Fray Jorge.

We quantified the behavior of actively foraging adult Tufted Tit-Tyrants and not those resting, primarily singing, or involved in other activities that might affect foraging behavior. Observations were conducted from 0700 to 1100 hrs under conditions of negligible wind. We regularly and repeatedly traversed the study site. Once a bird

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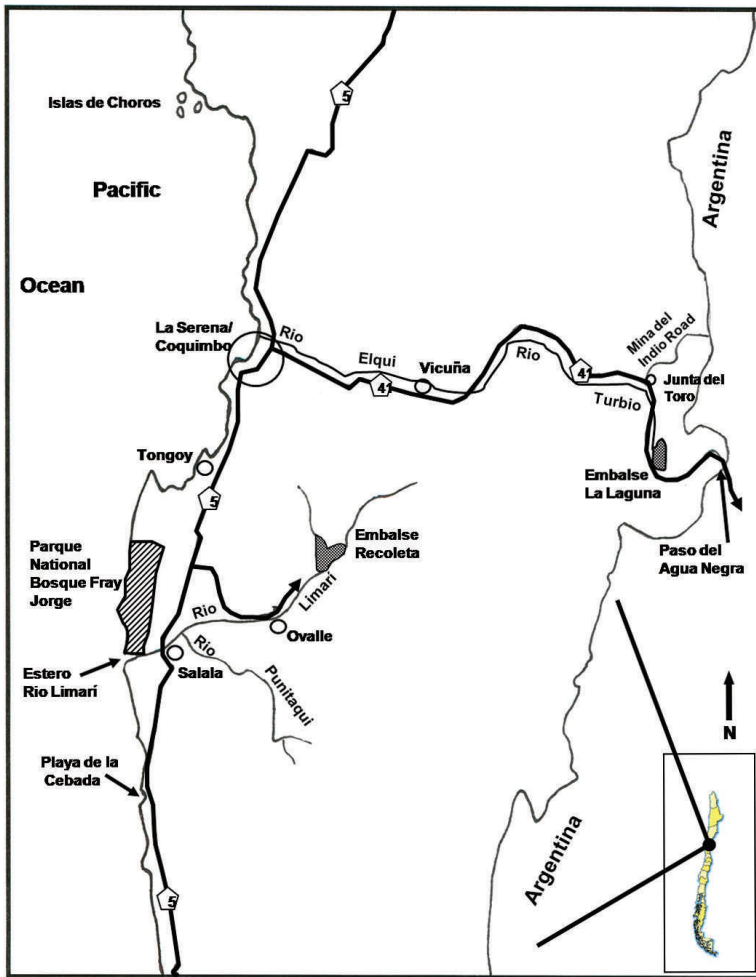


FIG. 1. Parque Nacional Bosque de Fray Jorge (study sites) along the coast of north-central Chile.

was found, we recorded sequential behaviors with a hand-held stopwatch. Initially, we did not record the first behavior observed, as this typically was the behavior that cued us to the bird, potentially introducing bias to our data (Franz 1984, Noon and Block 1990). We tracked the bird as long as we could record behavior. If the bird was lost (usually due to dense scrub), we stopped the timer until the bird was relocated, when we would start again (but ignoring the first behavior noted). The sequence of observations recorded was considered a single foraging bout. We recorded the species of shrub used (multiple plant species could be recorded per bout) as well as all foraging behaviors during the course of each bout. We adjusted methods in 2004 to record the first behavior observed allowing us to test suggestions

that sequential events by an individual bird would bias the overall total data set (Rabenold 1978, Franz 1984). We used behavioral categories outlined by Fitzpatrick (1980); specifically, fly-catching, hover gleaning, and perch gleaning. We also noted whether birds were alone, in pairs, or family groups, and if they joined mixed-species foraging flocks. We recorded observations of behavior associated with foraging birds including inter- and intraspecific foraging associations, agonistic behavior (chases, posture changes, vocalizations, and physical attacks), and search time. These data were used to describe foraging behavior, supplementing quantifiable data. Most foraging records were written in field books, but some were documented using a hand-held cassette recorder and later transcribed.

We measured population density using data from 32 point count stations on eight transects spanning ~7 km (north-south) in the Quebrada de las Vacas. Estimates were based on 8-min variable distance estimation following Bibby et al. (2000). These data were gathered from transects counted three times a year in August, October, and July from 2004 through 2007. Transects were surveyed twice each sampling period. All surveys were conducted in the morning (before ~1000 hrs) and were limited to days with low wind (Beaufort scale <2). We estimated detection functions and quantified density with program DISTANCE 5.0, Release 2 (Thomas et al. 2006).

We characterized the habitat using paired 5 m line-intercept transects at each avian point count station (32 sampling points). This method is most suited for shrub communities where cover and structure are goals of the assessment (Bauer 1943, Mueller-Dombois and Ellenberg 1974). We recorded the species, length of transect intercepted by the plant, and the maximum width of the plant perpendicular to the transect line for each individual plant overlapping the transect, and estimated ground cover following Cox (1996).

## RESULTS

We recorded 94 individual foraging bouts, comprising 17,788 sec of observations and 709 prey-captures. The time observing birds averaged 189 sec (range = 16–780 sec) per individual foraging bout.

**Density and Social Tendencies.**—Population densities showed marked temporal variation with no clear seasonal patterns; summer densities were not significantly higher than those in winter ( $t$ -test;  $t = 1.18$ ,  $df = 6$ ,  $P = 0.2842$ ; Fig. 2). Tufted Tit-Tyrants were ubiquitous on all transects and were recorded at nearly every point count station at least once annually. Birds were evenly distributed among the Matorral and were not observed in flocks.

Tufted Tit-Tyrants were not social in their foraging associations. We did not observe Tufted Tit-Tyrants in mixed-species foraging flocks or in groups of more than three individuals (48, 17, and 4 observations of 1, 2, and 3 individuals, respectively). Birds in pairs foraged leapfrog style, and not more than a few shrubs distant from one another. They maintained constant contact visually and with a soft, rolling “perr-reet” vocalization. Birds generally approached a shrub low to the ground, and then foraged upward

towards the crown. Once on top, they called and made visual contact with their foraging partner. Foraging pairs were observed in summer and winter; presumed family groups of three birds were observed only in the post-breeding period (Feb surveys). Tufted Tit-Tyrants also exhibited strong intraspecific aggression, defending what appeared to be foraging territories. We observed 18 agonistic interactions during summer (15 in 77 foraging bouts) and winter (3 in 17 foraging bouts). Agonistic behavior included rapid calling and displacement behavior (bill wiping, wing flaring), crest raising, chases through shrubs, physical attacks, and 12 times involved a pair defending their space. Once the intruder moved away, the defending pair returned to their foraging activities. We did not observe interspecific aggression despite the presence of other insectivores including the Chilean House Wren (*Troglodytes aedon chilensis*) and Plain-mantled Tit-Spinetail (*Leptasthenura aegithaloides*).

**Shrub Selection by Tufted Tit-Tyrants.**—Tufted Tit-Tyrants used plants largely in proportion to their availability (linear regression;  $F = 16.28$ ,  $df = 12$ ,  $P = 0.0020$ ; Fig. 3). They were observed foraging primarily in three species of shrubs (*Adesmia*, *Baccharis*, and *Porlieria*), which accounted for 76% of foraging observations but only 58% of shrub cover (Table 1), suggesting a moderate amount of selectivity. The former two were selected during foraging activities; *Baccharis* and *Adesmia* were the focus of 26 and 24% of foraging activity, respectively, but comprised only 9.2 and 15.5% of shrub cover, respectively. *Porlieria* was under-used with 26% of the observations but 33% of shrub cover (Table 1). A fourth shrub, *Chenopodium*, was moderately abundant (11% of shrub cover) but received <1% of foraging visits (Fig. 4).

We lacked sufficient observations in winter to test for seasonal differences, but available data strongly suggested seasonality in foraging. Summer foraging emphasized *Baccharis* (32% of summer observations), *Porlieria* (29%), and *Adesmia* (17%), while winter foraging was strongly directed towards *Adesmia* (52%), followed by *Porlieria* and *Proustia* (16% each). *Baccharis* was used only in summer, as were a number of low growing, semi-open, flowering plants (Fig. 4).

**Method of Prey Capture.**—Tufted Tit-Tyrants located insects with visual searching and used three methods to capture prey: perch glean- ing,

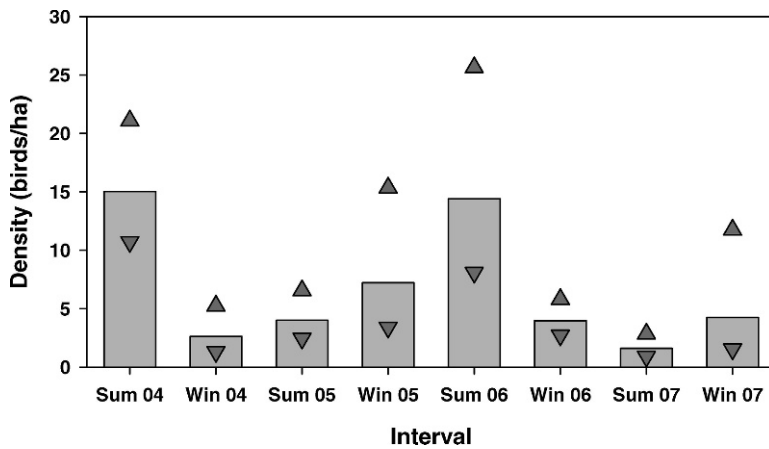


FIG. 2. Seasonal density (birds/ha) of Tufted Tit-Tyrants at Parque Nacional Bosque de Fray Jorge, Chile, 2002–2004. Estimated density (vertical bars) and 95% confidence limits (triangles) using Program DISTANCE.

hover glean, and flycatching (Fig. 5). They averaged  $3.1 \pm 1.8$  (SD) prey attacks/min ( $n = 700$  prey capture attempts). Perch glean was the primary mode of prey capture (47% of total captures) and was generally initiated from foliage (Fig. 5); the typical foraging posture was an upright position with the wings dropped below the tail and the tail pointing downward. They frequently sat quietly for 3–5 sec while scanning upward into vegetation.

Hover glean comprised 31.5% of observed prey-capture events (Fig. 5); in the most common maneuver, the bird flew upward from a perch to

strike prey from vegetation surfaces as the bird hovered up to 2 sec. Tufted Tit-Tyrants usually moved to a new perch after a hover glean event. They also frequently used simple upward strikes, leaping up and gleaning prey off of a substrate without hovering.

Flycatching was the least used capture method (21.5% of recorded capture events) (Fig. 5), and included both short sallies (flight chases <3 m from perch usually resulting in flying back to or near the take-off point) and long sallies (flight chases >3 m from perch and flight usually involving a pursuit of insect prey followed by

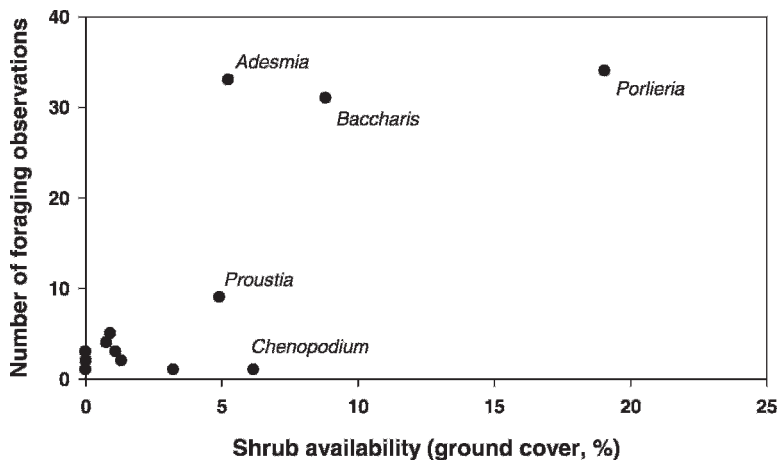


FIG. 3. Number of foraging observations by Tufted Tit-Tyrants as a function of aerial cover of focal plant species (>1 plant is generally visited/foraging bout, recorded as separate observations); plant species used largely in proportion to availability (linear regression;  $F = 16.28$ ,  $df = 12$ ,  $P = 0.0020$ ).

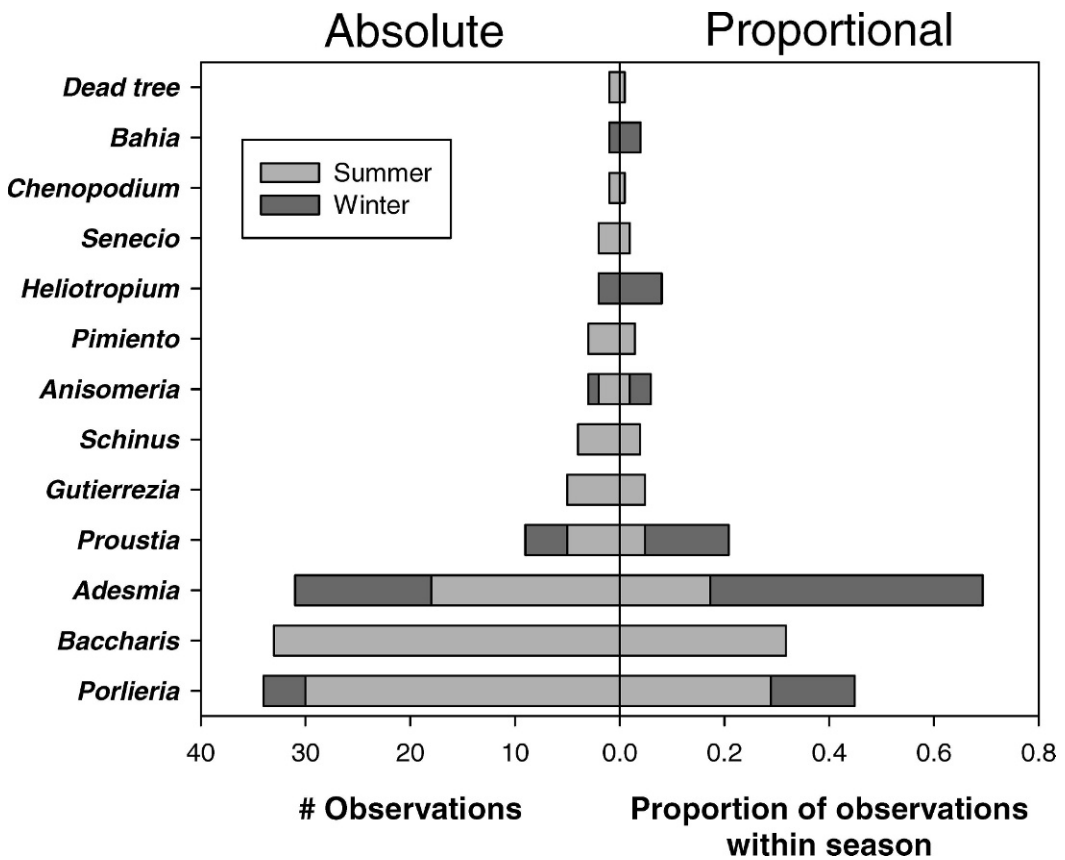


FIG. 4. Distribution of foraging observations by plant species and season.

perching in a different shrub). Short sallies were slightly more common than long sallies (56.2 vs. 43.8% of flycatching events). On one instance, a pair was observed flycatching in a *Baccharis* shrub with a swarm of gnats. One bird quietly waited in the interior of the shrub while the other repeatedly sallied upward to capture gnats from the swarm. After a dozen sallies, the upper bird retired into the center of the shrub and the other bird took its place at the top, feeding in a similar manner.

Foraging interpretations were not affected by using cumulative observations rather than only first observations; the proportion of observations changed slightly, but the rank order remained the same with each data set (correlation,  $r^2 = 0.93$ ). The two dominant behaviors comprised the vast majority of observations in both data sets, 78.0 and 78.4% of observations using first observation only and cumulative observations, respectively.

## DISCUSSION

Our data confirm the characterization of Tufted Tit-Tyrants as primarily a perch gleaner (Wetmore 1926, Smith 1971, Fitzpatrick 1980). Tufted Tit-Tyrants procure prey predominantly from within or along the edges of shrubs, and they superficially resemble regulids and parids, both of which are perch gleaners (Austin and Smith 1972, Robinson and Holmes 1982, Franzreb 1984, Kleintjes and Dahlsten 1994). However, upon closer examination, they are more variable in foraging behavior, and more typically a tyrannid. First, Tufted Tit-Tyrant are active but mostly deliberate foragers, using 3–5 sec search times when hunting for prey items. Additionally, their prey attack frequency ( $3.1 \pm 1.8/\text{min}$ ) is comparable to those reported for other small flycatchers (Fitzpatrick 1980, Robinson and Holmes 1982, Keast et al. 1995), but significantly lower than those recorded for kinglets ( $9.3 \pm 8.2$  attacks/min;

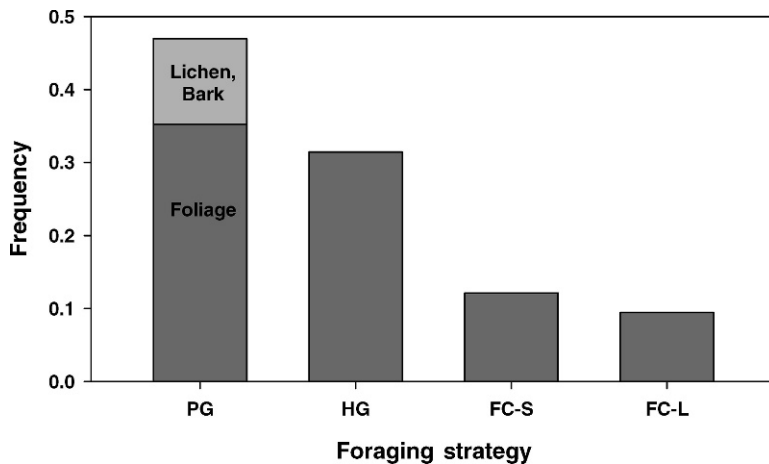


FIG. 5. Proportion of foraging observations that were perch glean (PG), hover glean (HG), and both short and long flycatching sallies (FC-S and FC-L, respectively). Perch glean is segregated by substrate (foliage vs. lichen or bark).

Keast and Saunders 1991). Search time was not reported in these studies, but higher prey attack rates coupled with high number of hops per minute indicate that kinglets use short search periods between prey attacks, differing from Tufted Tit-Tyrants (Robinson and Holmes 1982, Keast et al. 1995). Parids are primarily perch gleaners, but differ in their foraging strategies by frequently hanging on vegetation tips; they rarely use flycatching or hover gleaning (Austin and Smith 1972, Robinson and Holmes 1982, Kleintjes and Dahlsten 1994).

Nearly all tyrannids use variable and sometimes lengthy search times as a distinctive component of their foraging strategy (Fitzpatrick 1980, 1981). Tufted Tit-Tyrants, for their size, use relatively long search periods before attacking prey. Search time is predicted to be proportional to body size among predators (MacArthur 1972), and Fitzpatrick (1981) confirmed this for tropical tyrannids. Tufted Tit-Tyrants are small birds (6.1 g at our study site;  $n = 11$ ), and our findings of search time (3–5 sec) and foraging strategy, predominately perch glean and, when hawking, using predominantly short-sally flycatching, fit Fitzpatrick's (1981) model predictions for a bird of this size.

Tufted Tit-Tyrants have a large geographical range, within which they occur in a variety of habitats, suggesting generalist foraging habits. Our data support this categorization in two ways. First, foraging was highly correlated with plant availability in Fray Jorge, as quantified by aerial cover (Table 1). Second, the species is able to

move and shift foraging preferences based on flowering and vegetative phenology (e.g., summer preference for *Baccharis*). This shift in response to flowering phenology was also documented for Tit-Tyrants and other insectivores in semi-arid scrubland in Argentina (Blendinger 2005). Tufted Tit-Tyrants show a preference for denser shrubs and can move quickly to avoid detection (Hilty and Brown 1986). Our observations indicate their small size and short wings make them agile and capable of moving in tight places, thus exploiting the interior of dense shrubs characteristic of Matorral. Tufted Tit-Tyrants forage in summer extensively amongst *Baccharis*, which grows densely in washes where water remains close to the surface. These dense thickets are visible from great distances and appear to be preferred foraging sites for many insectivorous birds (A. Engilis Jr., pers. obs.). Tufted Tit-Tyrant foraging during winter was largely confined to the three most common shrubs at Fray Jorge, and focused primarily on *Adesmia*, a deep-rooted plant that flowers both in winter and summer.

Our observations of foraging associations indicate this species at Fray Jorge feeds primarily in pairs or small family groups (the latter during the post-breeding period). We did not observe the species in mixed species flocks in the Park. In south-central Chile, the Tufted Tit-Tyrant is reported to join mixed flocks, particularly with Thorn-tailed Rayadito (*Aphrastura spinicauda*), sometimes in numbers of 30 individuals in a flock (C. F. Estades, pers. comm.).

Population densities at our site were much



TABLE 1. Dominant plant composition of the Matorral habitat in the Quebrada de las Vacas, Parque National Fray Jorge, Chile. Aerial coverage is summed across all 32 point count stations.

Scientific name	Chilean name	Coverage, m <sup>2</sup>	% Cover
<i>Porlieria chilensis</i>	Guayacán	190,525	33.42
<i>Adesmia bedwelli</i>	Adesmia	88,181	15.47
<i>Chenopodium petiolare</i>	Chenopodium	61,703	10.82
<i>Proustia pungens</i>	Proustia	49,201	8.63
<i>Baccharis linearis</i>	Romerillo	52,469	9.20
<i>Bahia ambrosioides</i>	Bahia	32,253	5.66
<i>Fluorencia thurifera</i>	Incienso	17,469	3.06
<i>Heliotropium</i> spp.	Helitropo	13,179	2.31
<i>Anisomeria littoralis</i>	Pircún	11,088	1.95
<i>Senna cummingii</i>	Alcaparra	9,853	1.73
Others (19 taxa)		53,134	9.32

higher than those reported elsewhere in Chile. Gonzales-Gomez et al. (2006) reported densities in fragmented Valdivian forests of southern Chile ranging from 0.18 to 0.60 birds/ha, and Estades and Temple (1999) reported 2.9 birds/ha. The latter authors reported 1.1 birds/ha in Valdivian open scrubland. These study sites were below 40° South latitude in a cooler and wetter climate; densities reported were from a single breeding season and did not account for annual variation in numbers.

Tufted Tit-Tyrants appear to forage as other small tyrannid flycatchers. It is a generalist species in terms of habitat selection and foraging activities, and occurs at relatively high densities in semi-arid, northern Chile where our study was conducted. Further observations should strive to clarify seasonal shifts in plant use, foraging in relation to flowering phenology, and effects of climate (e.g., El Niño Southern Oscillation) at this semi-arid site. The apparent defense of foraging territories year round also requires additional study. Tufted Tit-Tyrants remain a conspicuous, focal species in Matorral shrublands; well suited for further attention in ecological studies.

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