The Condor 100:641-653

PATTERNS OF ACTIVITY, FLOCKING, AND HABITAT USE IN PARROTS OF THE PERUVIAN AMAZON[1]

JAMES D. GILARDI[2] AND CHARLES A. MUNN[3]
Section of Evolution and Ecology, University of California, Davis, CA 95616

Abstract. We explored patterns of flight activity, flocking, and habitat use in a diverse community of parrots in an Amazonian lowland forest. Parrots were most active just after sunrise with a second peak of flight activity following a mid-day lull. *Brotogeris* spp. were exceptional, being most active in the early afternoon. Among the nine genera studied, we observed marked differences in where the birds flew relative to the canopy. Body size was a poor predictor of flight height, although it was strongly and inversely correlated with flock size. Most parrot species flew in groups of one to four individuals, suggesting that mated pairs are stable and that family groups remain together post-fledging. Flocks were exclusively monospecific except when the birds were foraging in trees or eating soil at clay licks. These forest-dwelling parrots did not show dramatic increases in flock size in the evening, reflecting the lack of communal and multispecies roosting observed in other parrots. Generally, the large- and mid-sized species of parrots were associated with high-ground forest, whereas smaller species favored transitional forest. Because daily ranging patterns for these parrots potentially include all habitats, these patterns of habitat use suggest selection for subtle differences among forest types. As expected, smaller species were less detectable at a distance than large species. Comparisons of size and detectability indicate that macaws can be reliably counted to a distance of 300 m, but 100 m may be more appropriate for the smaller and low-flying genera. In sum, we found that observing parrots from the canopy is a useful method for quantifying parrot activities in a closed-canopy system, and that these forest-dwelling parrots are markedly less social than their counterparts on islands and in more open habitats. Patterns of flight behavior, habitat preferences, and the body size to flock size relationship invite further studies on the roles of predation and resource availability in the structuring of parrot communities.

Key words: activity patterns, flock size, habitat use, nonbreeding behavior, parrots, roosting sociality, survey methods.

INTRODUCTION

Psittaciformes, one of the most diverse orders of birds (> 330 spp.), occur primarily in Australia, the Neotropics, and to a lesser extent, tropical Africa and Asia (Forshaw 1989). Although historically and currently familiar as pets (Hargrave 1970), the ecology of wild parrots remains poorly known (Forshaw 1989). In recent years, several Neotropical and Australian parrots have been sufficiently well studied to reveal a few ecological patterns (Saunders 1980, Snyder et al. 1987, Rowley 1990). Parrots generally feed on seeds and fruit, have low reproductive output, are long-lived, and occupy a variety of ecosystems from grasslands to tropical forests. The well-studied Neotropical species occur either on Caribbean islands (Snyder et al. 1987) or on the continent in habitats that are either dry, open, disturbed, or all three (Waltman and Beissinger 1992, Morales et al. 1994, Martuscelli 1995). In contrast, most Neotropical parrots occur in continental forest with closed canopies, and these populations remain largely unstudied due to the difficulties of observing, marking, and following birds in these habitats.

Manu National Park in the Peruvian Amazon presents an ideal opportunity to investigate an intact parrot community in a closed-canopy ecosystem; the park is essentially free of the poaching, logging, and hunting found elsewhere in much of the forested tropics (Terborgh 1983). In the lowland area, the historic meandering of the Río Manu has created a complex mosaic of habitats such that the forest type in a given location is largely determined by its altitude relative to flood level and river history (Salo et al. 1986). Sixteen parrot species are common along the Río Manu, ranging from sparrow-sized *Forpus sclateri* to *Ara chloroptera,* one of the largest flighted parrots weighing just over 1 kg (see Table 1 for common names).

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[1] Received 19 January 1998. Accepted 10 July 1998.

[2] Current address: Wildlife Preservation Trust International, 2320 Amapola Dr., Davis, CA 95616, e-mail: gilardi@mother.com

[3] Wildlife Conservation Society, 185th St. and Southern Blvd., Bronx, NY 10460.

As part of a broader investigation on the ecology of macaws, this study examined the diel activity patterns, flocking, and habitat use of the parrot community residing in this lowland rainforest. The study was conducted in the nonbreeding season during the driest months of the year in Manu (June–August), a period that presents frugivores with minimum food availability in all habitat types (Janson and Emmons 1990). Here we asked: when are different species active, do all species form flocks and what are those flocks composed of, to what extent do species favor particular habitat types within the forest, and how reliably can one count parrots in intact forest?

METHODS

Manu National Park lies on the eastern slope of the Andes in southeastern Peru (11°57′S, 71°17′W), the lowland areas of which are continuous rainforest interrupted only by rivers and oxbow lakes (elev. ~ 300 m). The study area (~ 800 ha) was selected for its proximity to a large clay lick where parrots visit daily to consume soil (Munn 1992), and includes habitat that is never directly influenced by flooding (upland forest), flat seldom-flooded terrain (high-ground forest), and seasonally inundated areas (transitional forest). The high-ground forest is actually very old, mature floodplain forest where the ground level matches the level of the most severe floods (see Terborgh 1983 for detailed habitat descriptions).

We established observation sites in emergent trees in each habitat type by climbing them with ropes and ascending devices (Munn 1991). Sitting on limbs of these trees 25–30 m above the forest floor, we chose a 180° clear view as the survey area to permit surveillance of birds up to a distance of 300 m. The trees were not randomly distributed in the habitat, nor were the viewing angles. Trees useful for surveillance are rare, so our intent was to establish a minimum of three trees in each habitat type with survey areas that encompassed representative forest. We sampled throughout daylight hours, but concentrated survey effort in the early morning when parrots were most active. We sampled for a total of 48 periods, each from 2–6 hr in duration from 29 June to 6 August 1992. Three observers collected the data (JDG, Bernat Garrigós, and Martin Heindl). All were skilled at visual and vocal identification of the study species before we began data collection. For each flock detected, we noted the species, number of birds, movement pattern, the closest distance they flew to the survey tree, and approximate altitude relative to mean canopy height. Because it is impossible to determine the sex or age of these parrot species by viewing external characteristics at a distance, we did not attempt to collect these data. If a flock was clearly oriented to or from a clay lick, or if it had been previously observed in a survey, we omitted it from the survey. These flocks were easily distinguished based upon flight orientation, flock size, and composition. To assess diel patterns of activity, we considered all flock observations, divided them into 10-min intervals, and plotted them against time of day. We made a rough estimate of the average height of the canopy, and then estimated where a particular flock was flying relative to that mean. Although this method lacks precision, error in these estimates is small relative to the variation among species, and thus the data are useful for interspecific comparisons.

To determine variation in social structure, we considered the correlation of body size with flock size (log mass vs. log mean flock size) and variation among species in mean flock size. Because the mean flock size provides an oversimplified picture of this variable, we also present the distributions of flock sizes of each species. To consider the possibility of communal roosting behavior, we looked for variation in flock size over the course of the day; because only *Amazona* spp. and the large *Ara* spp. showed evidence of such variation, they are the only two presented. Because of the small sample size, the disjunction in the *Amazona* data, and the fact that various statistical tests of diel flock size variation yield different results, we present these data without extensive analysis.

To examine species differences in habitat use, we evaluated data from surveys that spanned the period of highest activity (06:30–09:30), and compared counts for each species in each habitat using multiway contingency tables. All birds moving through the survey area were counted whether they perched in the habitat or not. Although this is not ideal, it was necessary to keep the sample size large enough to allow basic comparisons among the habitat types. Naturally, if movements of birds through the habitats were unrelated to use of that habitat, including fly-through data would in most cases weaken differences rather than strengthen them. We conducted 10–13 morning surveys in each habitat with roughly equal time spent in each survey tree, and equalized these data so that each habitat type received identical survey effort. We grouped the species into three size categories (large, medium, and small) to aid interpretation of the models. We tested each species × habitat table using the BMDP 4F procedure to test for homogeneity among counts, and to generate standardized deviates that indicate the contribution of a given cell to the overall effect. This analysis tests for differences among species, differences among habitats, and whether these effects interact. We used a forward selection model which adds the next most significant effect until adding effects does not significantly improve the fit of the accepted model (Christensen 1990).

To evaluate the effectiveness of surveying from the canopy, birds were grouped into three distance categories based upon how closely they flew to the survey tree: 0–100 m, 101–200 m, 201–300 m. The proportion of birds encountered in each category was then plotted against distance, and we calculated the slope of those three points. If one assumes that birds encounter the survey area from random directions, that they travel in a straight line, and that all birds are detected, then the likelihood of seeing a bird in each category is equivalent (despite the differing areas). Thus, perfect detectability would yield a slope of zero, and if detectability decreases with distance, the slope would become increasingly negative. If birds do not fly in straight lines (and of course they do not), then the detection probability should actually increase with distance from the survey tree because of the greater perimeter of the more distant categories. For this analysis of detectability, we grouped similarly-sized birds to increase sample size and compared the slopes of these species groups plotted against body size.

RESULTS

PATTERNS OF ACTIVITY AND FLOCK SIZE

Diel variation in activity was similar among nearly all species, showing a peak in the morning and again in the late-afternoon (Fig. 1). However, *Brotogeris* individuals were most active during mid-afternoon between ~13:00–15:00. We observed considerable variation in the altitude that species flew relative to the canopy (Fig. 2). Although birds within a genus flew at similar heights, body size was a poor predictor of this behavior ($R^2 = 0.036$, $P = 0.5$).

Most parrots traveled in small flocks of one to four individuals. All species of macaws and amazons showed similar distributions of flock size (Fig. 3A). These parrots primarily occurred in pairs, but occasionally three to five birds were seen in a flock, suggesting small family groups. Mid-sized parrots showed more diversity in flock sizes than either the larger or smaller species (Fig. 3B). Single individuals of *Pionus menstruus* and *Pionopsitta barribandi* were the most common "flock" encountered, and both species distributions tapered off at approximately five individuals. Individuals of *Pionites leucogaster* were more social and were most often seen in groups of 4–6 and occasionally 10 individuals. *Aratinga weddellii* showed a peak at two–three and five individuals, again suggestive of pairs or small family groups. The most atypical species was *Aratinga leucopthalamus*; more than half of the flocks seen contained 8–17 individuals and one flock comprised 32 birds. Along with their exceptional flight height, this flock size distribution suggests that these birds were flying through the area; they were seldom seen perched in these habitats and, although they do eat soil (Munn, unpubl. data), they did not use the clay licks in our study area. The smallest species moved about in small flocks similar in size to those of the large species: most often in pairs or small groups of three–seven birds, again suggesting family flocks (Fig. 3C).

Body size was a surprisingly good predictor of flock size, explaining nearly 40% of the observed variation (Fig. 4). We did not observe multispecies flocks except when birds were actively foraging in trees or eating soil at clay licks.

In general, we saw little evidence of birds aggregating at roosts in the evening, or groups leaving such aggregations at dawn. The *Amazona* spp. showed slight increase in mean flock size to about five birds per flock in the evening (combined to increase the sample size, Fig. 5A). In contrast, the large macaws showed the opposite trend, with the mean flock size decreasing between 15:00 and 17:30 (all *Ara* spp., excepting *A. severa,* Fig. 5B). Despite the sample sizes and other analytical issues, these results clearly indicate that these Amazonian parrots at this

TABLE 1. The parrots of Manu, Peru: body sizes, flock sizes, and relative abundances.

	Weight (g)[a]	Abundance (flocks hr^{-1})	Flock size (mean ± SD)	Abundance (indiv. hr^{-1})
Red-and-green Macaw *Ara chloroptera*	1,250	0.70	2.2 ± 1.0	1.51
Blue-and-yellow Macaw *Ara ararauna*	1,125	0.77	2.4 ± 1.3	1.81
Scarlet Macaw *Ara macao*	1,015	1.05	2.6 ± 1.6	2.73
Mealy Parrot *Amazona farinosa*	800	1.82	2.7 ± 2.4	5.58
Yellow-crowned Parrot *Amazona ochrocephala*	510	0.20	1.8 ± 0.5	0.41
Chestnut-fronted Macaw *Ara severa*	430	0.56	2.6 ± 1.3	1.46
Blue-headed Parrot *Pionus menstruus*	293	2.76	2.4 ± 3.5	6.69
White-eyed Parakeet *Aratinga leucophthalamus*	190	0.17	9.0 ± 7.0	1.49
White-bellied Parrot *Pionites leucogaster*	155	0.39	5.2 ± 3.0	2.02
Orange-cheeked Parrot *Pionopsitta barrabandi*	140	0.36	2.3 ± 2.0	0.84
Dusky-headed Parakeet *Aratinga weddellii*	110	0.82	4.9 ± 3.6	4.04
Rock Parakeet *Pyrrhura rupicola*	75	0.14	2.9 ± 2.2	0.55
Painted Parakeet *Pyrrhura picta*	67	0.65	4.7 ± 4.7	3.07
Cobalt-winged Parakeet *Brotogeris cyanoptera*	67	0.45	4.2 ± 2.5	1.88
Tui Parakeet *Brotogeris sanctithomae*	64	0.08	3.8 ± 2.8	0.31
Brotogeris spp. *Brotogeris* spp.		5.46	4.6 ± 5.5	25.13
Amazonian Parrotlet *Nannopsittaca dachilleae*	41.7[b]	present	present	present
Dusky-billed Parrotlet *Forpus sclateri*	25	0.02	6.6 ± 2.2	0.13

[a] Terborgh et al. 1990.
[b] O'Neill et al. 1991, present but not detected in censuses.

time of year are not forming large roosting aggregations nor are they gathering in multispecies groups.

PATTERNS OF HABITAT USE

Although the three habitats studied, upland, high-ground, and transitional forest, appear superficially similar, many species showed distinct positive or negative associations with particular habitats. In each group of parrots tested, large, mid-sized, and small parrots, the saturated model proved the best fit (species × habitat, $P < 0.001$). This indicates that there were significant differences in abundance among species independent of habitat, that there were differences in habitat-use independent of species, and that these effects interact.

Of the large parrots, the high-ground forest was most preferred, followed by transitional and finally upland forest (Table 2). The standardized residuals show that *Ara chloroptera* preferred upland habitat and, along with *A. macao* and *A. ararauna,* avoided transitional habitat. *Ara ararauna* was the only large parrot to strongly prefer the high-ground habitat, whereas *A. severa* only weakly avoided upland areas. The amazons preferred the transitional forest and avoided the high ground habitat; however, *Amazona ochrocephala* was uncommon in all habitats.

Mid-sized parrots exhibited similar overall

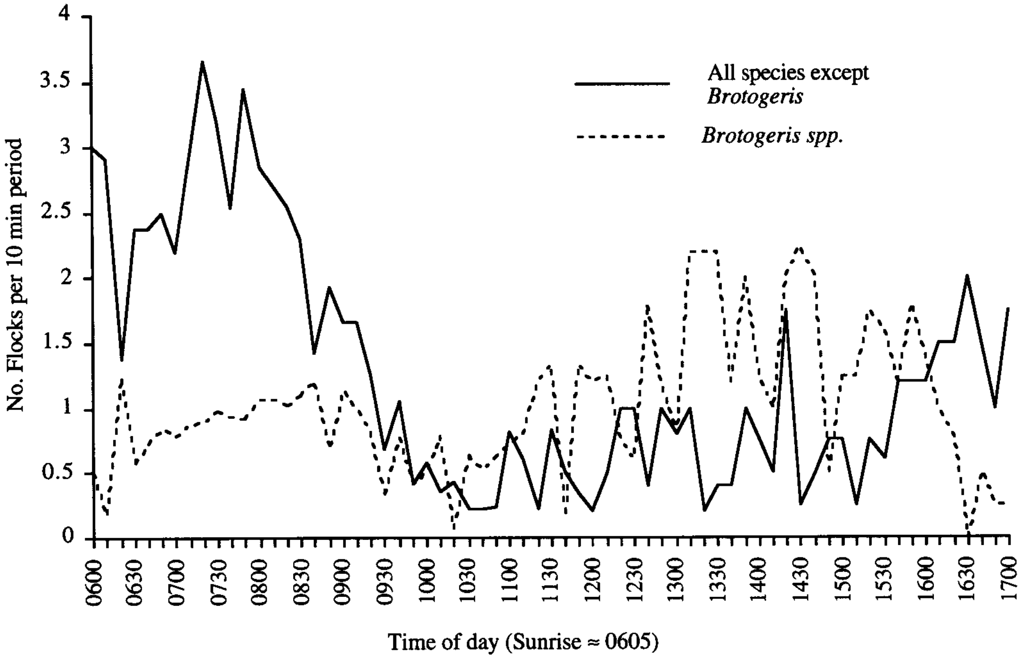

FIGURE 1. Diel variation in parrot flight activity observed from the canopy in Manu, Peru 1992. The genus *Brotogeris* is plotted separately to highlight its unique afternoon activity peak.

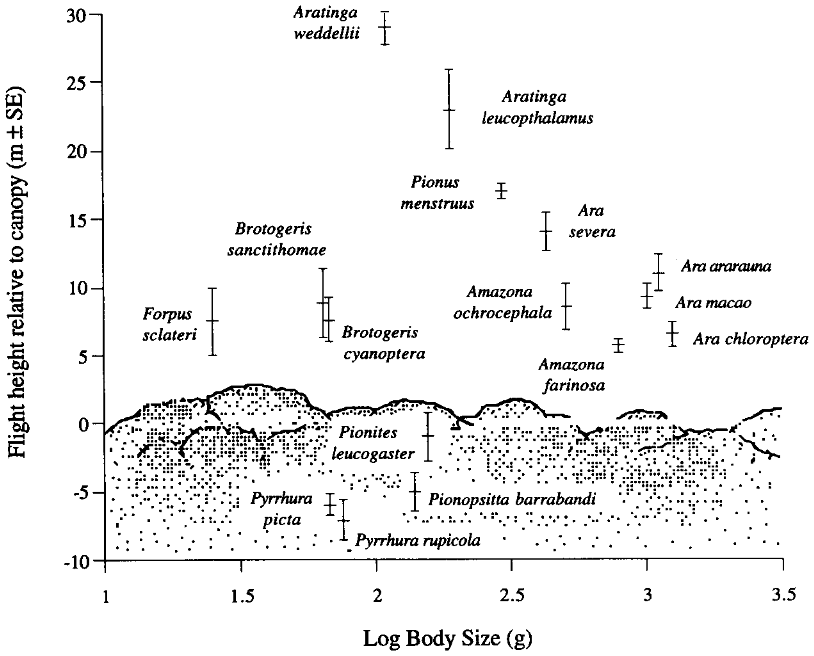

FIGURE 2. Body size versus flight altitude in Amazonian parrots, Manu, Peru. Note that body size is a poor correlate of flight height, but that congeners fly at very similar heights.

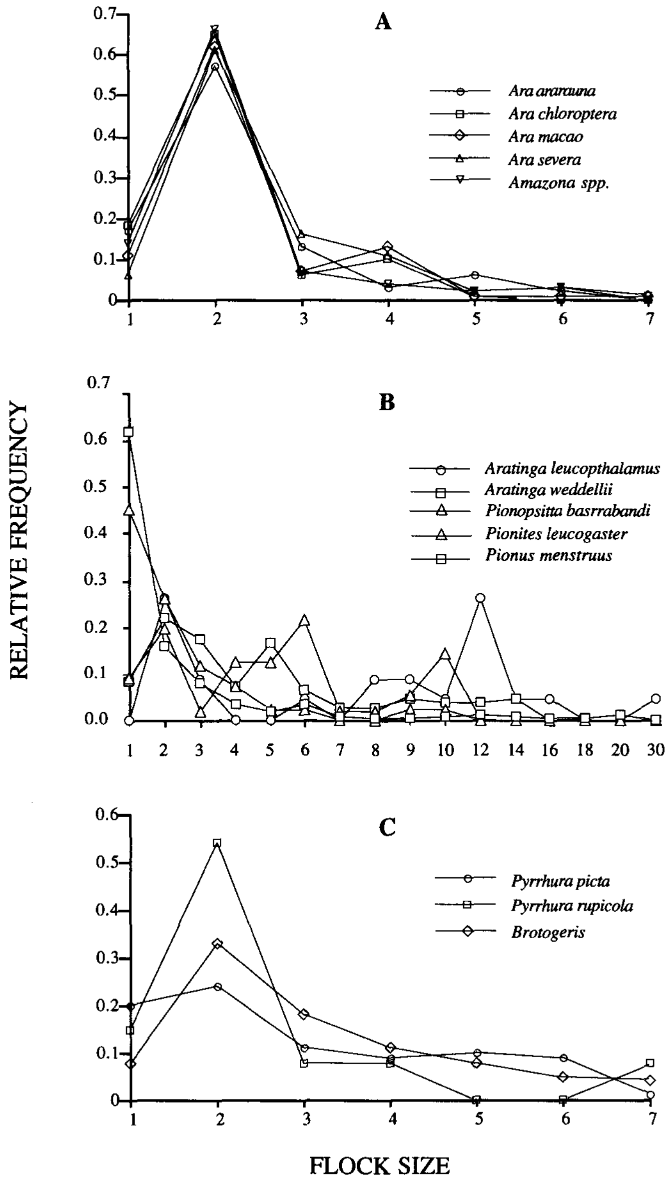

FIGURE 3. Flock size distributions of large parrots (A), mid-sized parrots (B), and small parrots (C) in Manu, Peru.

patterns of habitat preference: high ground > transitional > upland forest (Table 2). *Pionopsitta barrabandi* strongly preferred high ground forest avoiding the other habitats almost completely. *Pionites leucogaster* preferred transitional forest, and *Pionus menstruus* was unique in this community, showing a strong association with upland habitat.

The smaller species generally avoided upland forest, although other habitats were used to a similar extent (Table 2). *Brotogeris cyanoptera* and *Pyrrhura* spp. showed a strong preference for transitional habitat, whereas none of these species showed particularly strong avoidance of any habitat. Clearly in this model, *Brotogeris* spp. was the most numerous group and essentially defined the background frequencies against which all the others were compared.

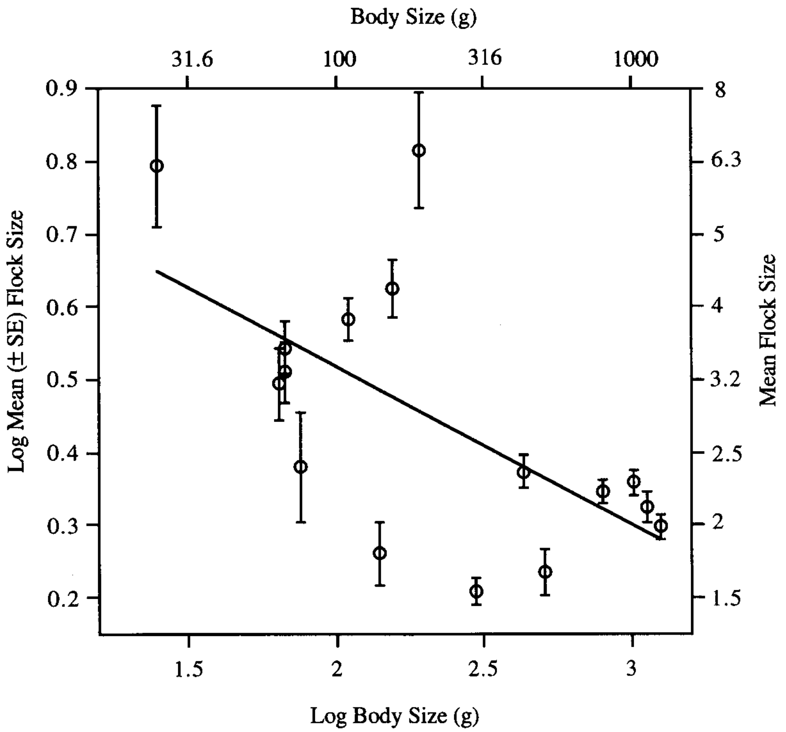

FIGURE 4. Mean flock size as a function of body size in Amazonian parrots ($R^2 = 0.38$, $P = 0.01$).

However, removal of this group had little affect on the standardized deviates.

SURVEY CONSIDERATIONS

Not surprisingly, we found that body size was an excellent predictor of detectability—larger birds being more detectable in the more distant survey categories (Fig. 6). Analysis of slopes of detectability revealed that only macaws were well detected out to 300 m; the slightly positive value suggests inaccurate distance estimates and/or nonlinear flight behavior. Finally, the two smallest but similarly-sized genera (*Pyrrhura* and *Brotogeris*) showed marked differences in slope, an observation which is consistent with their corresponding differences in flight height relative to the canopy (means +8.2 m and −6.55 m, respectively).

DISCUSSION

Our principal goal in this study was to address basic questions of nonbreeding behavior of a community of rainforest parrots: when birds are active, with whom do they associate intra- or interspecifically, to what extent they prefer particular habitat types, and finally, whether we can gain insight into these questions by working from the rainforest canopy.

PATTERNS OF ACTIVITY

Diurnal birds are particularly active in the morning and afternoon (Robbins 1981), and forest-dwelling Neotropical parrots appear to be no exception. Similar patterns of activity have been noted in three of these parrot genera elsewhere in the Neotropics: *Amazona vittata* in Puerto Rico (Snyder et al. 1987), *Ara rubrogenys* in Bolivia (Pitter and Christiansen 1995), and *Aratinga canicularis* in Guatemala (Hardy 1965). Outside of the Neotropics, similar patterns in activity were seen in cockatoos, rosellas, lorikeets, and budgerigars (Wyndham 1980, Wyndham and Cannon 1985, Rowley and Chapman 1991). Seasonal variation in activity has been explored in three Australian species and the mid-day lull in activity is clearly associated with the warmer months (Westcott and Cockburn 1988, Emison 1994).

Explanations for such patterns of activity typically invoke temperature and/or predation

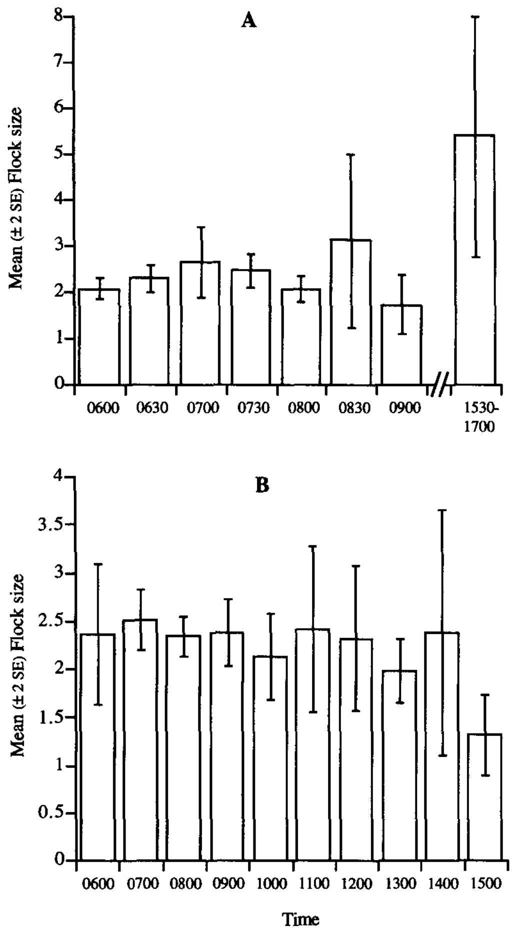

FIGURE 5. Diel variation in *Amazona* spp. (A) and *Ara* spp. (B) flock sizes. Note the lack of amazon flocks between 09:30 and 15:30, thus the differing time axes.

(Westcott and Cockburn 1988). That is, activities requiring elevated metabolic rates are best done when temperatures are relatively mild, or when predators are least active, or both. Given that parrots generally do not fly at night, the early morning hours provide a relatively cool and well-lit opportunity for foraging. In Manu, temperature may explain the morning activity peak, but all species show afternoon activity well before the temperature drops in the evening. In contrast, *Brotogeris* spp. were active throughout the day, with maximum activity in the hot afternoon. Because these birds are the smallest genus for which we have good data, this finding suggests that the smaller parrots may be more physiologically capable of maintaining flight activity in the heat of the day. They may thereby avoid predation by several species of diurnal raptors which prey on *Brotogeris* spp. in this area (Robinson 1994). However, the relationship of body size with heat gain during exercise in a high-humidity environment is unclear (Eckert and Randall 1988; T. Bucher, pers. comm.).

An alternative explanation for the observed morning and afternoon activity may not relate to temperature or predation. With abundant food in the tropical forest, most parrots feed to satiety in the morning, rest for several hours, and end the day with a second feeding bout in the late afternoon. Not only do foraging patterns in Manu support this hypothesis (unpubl. data), but most captive birds show a similar pattern despite ad libitum food, constant temperature, and no risk of predation (L. Loviatt, pers. comm.). For wild parrots in open or dry habitats, where food may be less abundant or more difficult to process, activity patterns may be different. Thick-billed Parrots (*Rhynchopsitta pachyrhyncha*), for instance, invest considerable time processing pine cones to extract seeds and in some cases spend the entire day actively foraging (N. F. R. Snyder, pers. comm.).

Where forest birds choose to fly relative to the canopy is presumably influenced by a combination of factors including temperature, predation, wing morphology, and flight duration. Although use of different strata within the canopy has received attention (Dunlavy 1935, Pearson 1971), where birds fly when moving through or above the canopy has not. One might predict that smaller species would respond to avian predation pressure by flying lower in the canopy, but our data show that body size is a poor predictor of flight height. If predation pressure is in general inversely related to body size, then it either is unimportant in this system, or has little influence on this aspect of flight behavior. Indeed, these birds presumably avoid predation in other ways—possibly through flock formation and rapid flight. The fact that birds within a genus chose similar flight paths suggests either similar ecology or morphological constraints, but further interpretation is speculative. The physical structure of the canopy sampled was superficially similar in all habitats; we saw nothing to suggest that birds altered their flight-height depending upon habitat type.

TABLE 2. Relative abundances of rainforest parrots among three habitat types in Manu, Peru. Species are grouped into three size-classes to aid in interpreting the contingency table analysis of each species group. The standardized deviates indicate how each cell diverges from the expectation of no preference among habitats, the proportion of flocks observed in a given habitat is shown parenthetically, and the number of flocks observed in surveys from 06:30–09:30 is summed for each species.

Large parrots	*Amazona* spp.	*Ara ararauna*	*Ara chloroptera*	*Ara macao*	*Ara severa*	Total
Habitat						
Upland	−0.1 (24.5)	−1.3 (17.1)	+2.8 (42.6)	+0.6 (27.8)	−1.9 (11.5)	−0.1 (25.0)
Transitional	+3.7 (48.6)	−2.4 (17.1)	−2.1 (18.0)	−2.2 (20.6)	+0.8 (40.4)	−2.3 (33.8)
High-ground	−3.2 (26.9)	+3.2 (65.7)	−0.2 (39.3)	+1.6 (51.5)	0.8 (48.1)	+2.1 (41.2)
Total flocks	208	70	61	97	52	488

Mid-sized parrots	*Aratinga leucoptera*	*Aratinga weddellii*	*Pionopsit. barrabandi*	*Pionites leucogaster*	*Pionus menstruus*	Total
Habitat						
Upland	−0.1 (28.6)	−1.4 (20.3)	−2.8 (3.1)	−1.2 (18.9)	+2.5 (38.5)	−3.0 (29.4)
Transitional	+0.3 (35.7)	+0.6 (35.1)	−3.2 (0.0)	+2.5 (54.1)	−0.2 (30.0)	0 (31.0)
High-ground	+0.2 (35.7)	+0.7 (44.6)	+5.2 (97.0)	−1.2 (27.0)	−1.9 (31.5)	+2.6 (39.6)
Total flocks	14	74	33	37	213	371

Small parrots	*Brotogeris cyanoptera*	*Brotogeris sanctithomae*	*Brotogeris* spp.	*Pyrrhura picta*	*Pyrrhura rupicola*	*Pyrrhura* spp.	Total
Habitat							
Upland	−1.5 (5.7)	−0.2 (12.5)	+0.2 (15.9)	+1.9 (26.0)	−1.4 (0.0)	−0.7 (10.7)	−1.7 (15.6)
Transitional	+2.4 (74.3)	+0.7 (62.5)	−1.2 (42.9)	−1.1 (36.0)	+0.6 (58.3)	+3.0 (85.7)	+4.4 (46.6)
High-ground	−1.7 (20.0)	−0.6 (25)	+1.2 (41.1)	0.0 (38.0)	+0.2 (41.7)	−2.9 (3.6)	−3.8 (37.8)
Total flocks	35	8	496	50	12	28	629

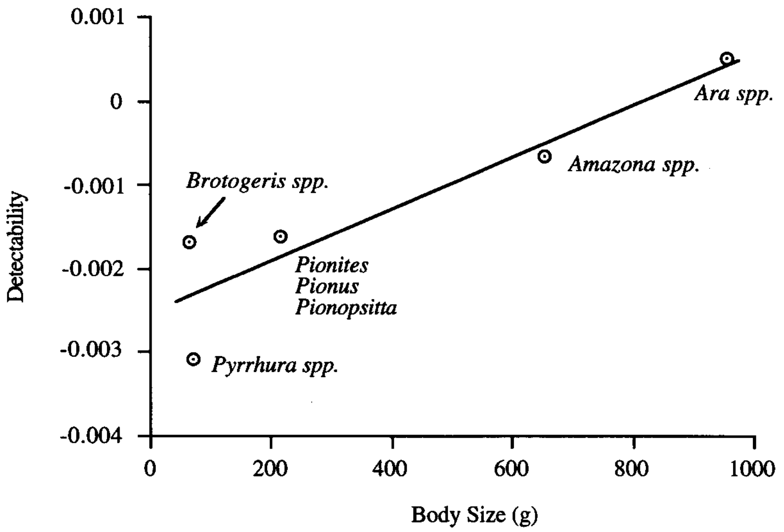

FIGURE 6. The effect of body size on the detectability of parrots in an intact Amazonian rainforest (R^2 = 0.84, P = 0.03). Detectability is calculated as the change in proportion of birds in each distance category (0–100 m, 101–200 m, etc.). Assuming random movements of birds and perfect detectability, the expected slope is 0 (e.g., *Ara* spp.). Slopes less than zero indicate that some distant flocks are going undetected (e.g., *Pyrrhura* spp.).

PATTERNS OF FLOCK SIZE

Parrots are social birds, some species forming flocks of thousands of individuals (Forshaw 1989, Emison et al. 1994). Brereton (1971) and Cannon (1984) hypothesized that, for Australian species, aridity was positively associated with flocking, whereas Westcott and Cockburn (1988) suggest that predation is a more important predictor of sociality in parrots. Because the Manu forests are on the wet end of this continuum, the small flock sizes we observed support aridity over predation as a determinant of flock size. However, whether Australian and Neotropical systems are directly comparable is unclear, and whether parrots in open and dry habitats in the Neotropics are more social than forest dwellers remains an open question.

Neotropical parrots show considerable variation in flock size. *Amazona vittata, A. ventralis,* and *A. leucocephala* consistently move in singles and pairs (Snyder et al. 1987), although all form large flocks of 10s to 100s of birds outside the breeding season (J. Wiley, pers. comm.). Hawk-headed Parrots (*Deroptyus accipitrinus*) move primarily in small flocks with occasional groups of up to 10 individuals (Strahl et al. 1991). Chapman et al. (1989) observed large flocks of 4–21 individuals (mean 8.1) of three species of parrots in dry forest in Costa Rica, perhaps hinting at a difference between dry or open habitat vs. humid forest. However, they were observing these large mixed-species flocks at foraging trees (Chapman, pers. comm.), which is consistent with what we observed at foraging events in Peru (unpubl. data). In a naturalized population of Mitred Parakeets (*Aratinga mitrata*), annual mean flock size varied from 10 to 20 birds and showed seasonal variation with the smallest flocks (mean ~ 5 birds) occurring during the breeding season (Collins and Kares 1997). Our observations of generally small flock sizes of parrots in the nonbreeding season therefore suggest that forest-dwelling parrots may be markedly less social than parrots in other habitat types.

The role of predation in determining flock size suggested by Westcott and Cockburn (1988) can not be entirely ruled out. Body size explained roughly 40% of the variation in flock size among parrots in Manu. If predation leads to flocking and if smaller species are more susceptible to predation, then one would predict what we observed—that smaller species would occur in larger flocks. However, this correlation may be an overestimate for two reasons. First, because birds within a genus tend to be similarly-sized, each species is not independent of its congeners (Harvey and Pagel 1991). Second, because small birds generally have larger clutch sizes, family flocks would be larger, independent of predation.

Whether these birds travel in pairs or families is perhaps more clearly answered by the distribution of flock sizes rather than mean flock size. For the large parrots, *Ara* and *Amazona,* the primary social unit appears to be the pair, or pairs with one to three additional individuals which are likely young of the year. Most flocks are clearly substructured into pairs and additional birds. When groups of *A. chloroptera* and *A. macao* visit the clay licks, they tend to arrive as adult pairs with or without dependent chicks (Munn 1992). If this adult-chick flock structure holds for *A. ararauna* (which do not visit the licks in Manu), then the existence of flocks of five birds suggests that they occasionally fledge three chicks. For most other species in Manu, flock size distributions are consistent with a family-group interpretation.

Flocking behavior also has been used as an indicator of communal roosting, which is widespread among parrots (Forshaw 1989). Chapman et al. (1989) found a significant increase in flock size as evening approaches, as well as nocturnal roosts of large numbers of individuals of four parrot species. Similar patterns of evening *Amazona* aggregations were observed in the Bahamas, Puerto Rico, and Guatemala (Snyder et al. 1987, Gnam and Burchsted 1991, Johnson and Gilardi 1996). Outside the Neotropics, communal roosting is widespread among parrots. Rainbow Lorikeets (*Trichoglossus haematodus*) form large flocks in the morning and evening (Utschick and Brandl 1989), and African Gray Parrots (*Psittacus erithacus*) form traditional roosts numbering in the hundreds (Serle 1965). The data are mixed for rosellas; Eastern Rosella (*Platycercus eximius*) flocks are largest in the early morning, but this pattern was not observed in Pale-headed Rosellas (*P. adscitus,* Cannon 1984). In southern California, roosting flocks of several *Amazona* species commonly number as high as 600 birds (Mabb 1997).

Surprisingly, in most parrot species in Manu, we found no evidence for increased flocking in either the early morning or late in the day. At least in the dry season, none of these species formed large communal roosts, although *Amazona* may gather in small groups. In contrast, at the foot of the Andes near Atalaya, Peru, *Aratinga* spp. and *Brotogeris* spp. form large early morning flocks and descend from higher elevations (Gilardi, unpubl. data). The most obvious differences between the unbroken lowland forest in Manu and most of the other Neotropical sites mentioned are the degree of disturbance, topographical complexity, or both. Manu is essentially flat and undisturbed by humans. Thus, when hills or isolated trees are available, parrots may perceive such sites as good or safe places to roost, and when these sites are unavailable, parrots simply do not congregate. Additional work in other lowland forested sites will surely clarify whether communal roosting is directly related to such habitat features.

PATTERNS OF HABITAT USE

Most work on habitat selection in birds focuses upon either macro- or microscale selection (Cody 1985). That is, territorial song birds establish their territories within a given habitat type, or foraging birds are observed using a particular portion of a tree or layer of the canopy (Terborgh et al. 1990). In contrast, most parrots fly over large areas within a given day, creating the opportunity for mesoscale habitat selection or choice among forest types. Despite the parrots' broad ranging patterns and a coarse presence-absence criterion for habitat use, it is surprising that many of the associations found in this study remain quite strong. In related studies of parrot habitat use, differences among habitats are clear. Puerto Rican Parrots showed marked variation in abundance among the four forest types surveyed and avoided dwarf forest altogether (Snyder et al. 1987). Ground Parrots (*Pezoporus wallicus*) are selective of different habitat types, and their preferences depend upon season and seed availability (McFarland 1991). Magrath and Lill (1985) also found Crimson Rosellas (*Platycercus elegans*) unevenly distributed among habitats and suggest that these patterns depended upon the season and age of the birds.

Despite the superficial similarity of the habitats in Manu, they differ profoundly in the plant species present and the plants' fruiting phenology (Foster 1990, Janson and Emmons 1990). As in many avian frugivores, the parrots are presumably following fruit resources, the availability of which is spatially and temporally variable. Pursuing this question further would require the cumbersome task of mapping unripe-fruit availability in multiple habitats among seasons and among years and then correlating these patterns with mesoscale parrot movements.

Finally, similarly-sized parrots were generally associated with the same habitat types. Parrots show neither intra- nor interspecific aggression at foraging sites; most foraging bouts end well before a tree is depleted of its seed crop, and surviving seeds usually become unavailable by ripening which makes them undesirable (unpubl. data). Thus the habitat use patterns and foraging behaviors observed in this study are consistent with the observation that tropical frugivores pursue superabundant resources, and generally do not exhibit interference competition (Fleming 1979). In contrast, Thick-billed Parrots (*Rhynchopsitta pachyrhyncha*) are often aggressive toward Acorn Woodpeckers (*Melanerpes formicivorus*) and squirrels at foraging sites, suggesting the possibility of a temperate-tropical gradient in interspecific competition over foraging resources (Miguel Angel Cruz-Nieto, pers. comm.).

SURVEYING

Given the range of body sizes and flight behaviors of the parrots in Manu, one would expect the observed correlation between these variables and detectability; both size and behavior potentially biasing counts in favor of large or high-flying species. Our results suggest that macaws can be reliably counted to a distance of 300 m, but 100 m may be more appropriate for the smaller and low-flying genera. The latter estimate is consistent with the findings of Casagrande and Beissinger (1997) who found 150 m to be an effective cut-off distance for the tiny (~ 30 g) parrotlets they were surveying. Assuming that detectability is unaffected by the forest types surveyed in Manu, the size and behavior biases are unlikely to affect the findings of this study because abundance comparisons were primarily within species. However, evaluation of relative abundances of differently-sized species are affected; thus, the relative abundances presented here (Table 1) are likely underestimated for small and low-flying taxa. Depending upon the study design, one might compensate for this bias by limiting survey area or adding a correction factor for such taxa.

Finally, given that macaws and other parrots appear to form stable family flocks, flock-size data may be a reliable estimate of breeding parameters that are otherwise difficult or impossible to gather. Within a species and population, comparisons among years may yield insight into the proportion of breeding birds, clutch size, and reproductive output of the population. To some extent, flock-size distributions have been used for these purposes in Manu (Munn 1992) and in other macaws in Bolivia and Costa Rica (Marineros and Vaughan 1995, Pitter and Christiansen 1995).

ACKNOWLEDGMENTS

We are very thankful for the assistance of many people in Manu, especially Mariana D. Valqui H., Estevan Huaman V., Juan Curaca, Dionisio Raimundi, and the Machiguenga community of Tayakome, Daniel H. Blanco Z., Patricia E. Villafuerte T., and Thomas H. Valqui H. We are especially thankful to Bernat Garrigós, Martin Heindl, and Ellen Andressen, who spent many buggy-hours in trees and on trails at the field site. Several people have improved this paper with gently-critical comments: Sean Duffey, Jim Quinn, Ian Rowley, Noel Snyder, Cathy Toft, Jim Wiley, and Tim Wright. We thank the Graduate Division, the Center for Population Biology at UC Davis, and the Wildlife Conservation Society for financial and logistical support of field work. Patagonia, BlueWater, and Black Diamond kindly donated equipment or made in-kind contributions.

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