TITLE: Cooperation, status, and altruism in a mixed society of Amazonian parrots

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ABSTRACT 186 words

Parrots are a highly intelligent taxon whose complex behaviors in wild societies require description. Here we observed 12 species of parrots, macaws, and parakeets in mixed flocks foraging on exposed cliffs in southeast Perú. For each species, we developed a single bootstrapped index of sociality from 9 derived metrics of abundance, chronology, functional roles, and agonistic interactions. This multivariate index emphasizes species that join flocks in large numbers, participate early, serve in functional roles, interact with others, and are socially dominant. We used Random Forest ("RF") algorithms to build nonlinear multiple regressions to assess and rank the influence of a suite of taxonomic and morphometric factors on sociality. The RF models performed well (R^2 = 0.96) and indicate species with smaller brains (controlled for body size) and lower dispersal abilities are most social, though the underlying mechanisms may be indirect. In addition, we document a distinct sequence of species flock participation where subordinate species serve as nuclear species that initiate flock assembly and foraging, while dominant species serve as sentinels, foraging after subordinates. This suggests cooperation in this mixed society features sequenced tradeoffs and reciprocal altruism.

INTRODUCTION 599 words

Animal societies occur in a variety of forms, taxa, and settings and are important in structuring ecological communities (Ehrlich and Ehrlich 1973, Emlen and Demong 1975, Van Schaik 1983, Holldobler and Wilson 2009, Doody et al. 2013). Cooperating groups are popular because they confer benefits for and reduces risks to member fitness, with the primary advantages being increased provisions and decreased depredation (Krebs and Davies 1993, Raihani 2021). For these reasons—and facilitated by their shared morphological and behavioral traits—most animal societies consist of a single species. Stable and highly organized mixed societies, however, are especially widespread in birds (Darling 1938, Morse 1970, Barnard and Thompson 1985, Chapman et al. 1989, Hart and Freed 2003) and particularly abundant in tropical forest songbird communities (Moynihan 1962, Munn and Terborgh 1979, Powell 1985, Thiollay 1999, Mangini et al. 2023).

Most descriptions of such "mixed flocks" classify groups based on their principal food resource or physical niche (Powell 1985, Terborgh et al. 1990, Mangini et al. 2023). For example, mixed flocks that cooperatively forage within a stable home range are distinguished from those that feed on prey fleeing from swarms of army ants (e.g., *Eciton burchellii*), and from those congregating at fruiting trees (Daily and Ehrlich 1994)—even though their species composition might overlap (Munn and Terborgh 1979, Powell 1985, Jullien and Thiollay 1998). In addition, mixed flocks that forage in the forest understory have a characteristically distinct microhabitat and composition than canopy flocks—even though both might be territorial and structured by nuclear, sentinel, and leading species (Munn and Terborgh 1979). Indeed, is it possible for all these kinds of mixed flocks to exist simultaneously, yet completely independently, in the same patch of forest (Terborgh et al. 1990).

While they share many traits with such mixed flocks, multispecies foraging groups of parrots (e.g., Chapman et al. 1989, Gilardi and Munn 1998) do not receive as much focus, encouraging descriptions of their occurrence, organization, and behavior. Conveniently, parrot flocks may be easily observed as they are conspicuous and often aggregate at geographically fixed food resources. Early naturalists, for example, commonly noted large Carolina parakeet (*Conuropsis carolinensis*) flocks at mineral licks in the United States (Wilson 1811, Harper 1857)—a trait that contributed to the species' exploitation and demise (Cokinos 2000). In Perú, mixed societies of parrots, macaws, and parakeets gather in large numbers, daily, at exposed cliff banks to forage on clays and minerals. Here, previous studies have documented broad visitation patterns, habitat use, and motivations for consuming clays by such parrot groups (Gilardi and Munn 1998, Gilardi et al. 1999, Brightsmith and Muñoz-Najar 2004, Brightsmith and Villalobos 2011). However, much remains unexplored about their structure, organization, and social status, as well as how cooperation, altruism, and vigilance (Trivers 1971, Daily and Ehrlich 1994, Clutton-Brock et al. 1999, Raihani 2021, Farine 2022) functions within these groups.

Through a partnership between an indigenous community, tourism business, and university researchers (Brightsmith et al. 2008, Stronza and Durham 2008) we studied mixed parrot societies along the Tambopata river in southeast Perú. We monitored parrot flocks and their behavior, expanded on previous methods to quantify bird sociality (Jullien and Thiollay 1998, Van Houtan et al. 2006), and documented cooperation, roles, and antagonistic interactions. We further used machine learning to explore how sociality might be explained by a suite of taxonomic and morphometric traits for each species. As a result, this study helps describe the dynamics of mixed parrot flocks, expands on the literature of mixed bird flocks, examines potential morphological factors encouraging geophagy, and explores how cooperation and altruism functions in different mixed animal societies.

METHODS 1554 words

Field Site & Species Monitoring

The Tambopata Research Center ("TRC", 13.136358° S, 69.609541° W) is in the province of Tambopata, department of Madre de Dios, in southeast Perú. Moist tropical broadleaf lowland forests—terra firme, várzea, and bamboo—characterize this hyperdiverse region (Erwin 1984, Foster et al. 1994). TRC lies within the 2,800 km^2 Tambopata National Reserve, immediately adjacent the Tambopata River and the 11,000 km^2 Bahuaja-Sonene National Park. Here human access, use, and resource extraction are controlled (Kirkby et al. 2010, Asner and Tupayachi 2017). Approximately 750 m south of TRC, along the river, the study site is a 10m tall × 100m wide cliff of exposed clay ("collpa").

During the dry season June–October 1999, we observed parrot activity (INRENA permit no. 53-99-9-INRENA-DGANPFS-DANP) from an observation blind at the collpa base, ~25m across a small stream (Fig. 1). All counts and behavioral observations were facilitated by binoculars (8×32, Leica, Trinovid BA), with camouflaged spotting scopes (15-40× zoom eyepiece, Bushnell, Spacemaster) and video cameras (Hi8 with 10× zoom, Sony, no. CCD-v801) stabilized by tripods (Velbon, no. EFL4). At 30 min before twilight (civil dawn data: https://www.timeanddate.com/), researchers began listening for the first audible parrot calls while hiking to the observation blind (Fig. 1a). During this hour, ≤ 15 species of parrots and macaws gather in the emergent trees and vegetation above the cliff. In the blind, we recorded the timing and composition of the first sortie that flies circles above the collpa (the "dance") searching for a place to land (Van Houtan 1999). When this lead group lands, the dawn flock begins. At 5 min intervals, we recorded the number of individual birds from each species on the collpa, until the flock disbands. Though the dawn flock activity required 2 observers, ≥ 1 remained until 16:00, recording sporadic parrot flocks throughout the day. This protocol preceded (Van Houtan 1999, Van Houtan and Alvarez-Loayza 2006) and was only partially followed by subsequent monitoring efforts (Brightsmith and Muñoz-Najar 2004, Brightsmith and Villalobos 2011).

In addition to bird counts, observers recorded flock disturbances, sentinel alarms, and agonistic interactions between species. Though birds may congregate in monospecific clusters on the collpa (e.g., Fig. 1b-d), they mix and interact, sometimes agonistically. When one individual displaces another (through gape lunges, bites, wing beats, body pushing (Serpell 1982, Marcuk et al. 2020), or by dropping debris) we recorded the "winner" and "loser" species. We also recorded flushes, defined as when > 50% of perched or foraging birds abruptly dispersed and—when possible—noted the likely visual or audio cause. For flushes preceded by alarms, we recorded the sentinel species (Fig. 1e). We reviewed 40 hours of recorded video to confirm field observations and record additional behavioral data.

Summarizing Flock Activity & Sociality

We develop quantitative metrics from several observed traits of flock participation. We characterize 9 components in 4 categories: (i) abundance, (ii) chronology, (iii) functional roles, and (iv) interactions (see Table 1). As we are interested in mixed-species dynamics, we restrict all analyses to observations of multi-species flocks.

To account for the broad range of species sizes (70–1200 g (Brightsmith and Villalobos 2011)), we describe abundance by biomass and separately by individuals, normalizing each by observer effort (hr^{-1} day^{-1}). Second, we calculate chronology across the full day and then within the span of the dawn flock. The former is the time of the maximum abundance (in 5-min bins) for each species. Due to the correlation between dawn and flock formation—Fig. 2, $R^2 = 0.77$, $p < 0.0001$—

we rescale this time series by dawn time. (By contrast, unadjusted clock hours contain seasonal artifacts.) The latter chronology metric is the time (scaled 0–1) representing the maximum value of a locally weighted regression (“loess” (Cleveland and Devlin 1988)) fit to dawn flock abundance. Third, for functional roles, we tabulate the raw occurrences where each species participated in the pioneering dawn dance sortie and separately as an alarming sentinel. Fourth, we developed 3 metrics to describe agonistic interactions. To account for status, displacement rate is the number of wins divided by the total interactions. Interaction rate is the number of interactions divided by total daily individual abundance for each species. Interaction breadth is the number of species interacted with divided by the total number of flocking species (*n* = 12). Table 1 summarizes these descriptions.

Non-parametric bootstrapping derived a single index of sociality from the observed traits. For each species, we sampled the full set of component values $n \times n$ times (9 recursive samples for each 9 components), with replacement, where each component is equally weighted by category (to account for the uneven distribution). We sum the results, divide by *n*, and replicate the process 2000 times. Each replicate, as a result, represents the average cumulative value of 9 randomized full series draws from the complete set of 9 independent metrics. The resulting values are a multivariate and representative index of parrot sociality.

	category		component	description
i.	abundance	1	biomass	aggregate biomass of birds of each species (kg hr-1 day-1), corrected for observer effort
	abundance	2	individuals	aggregate number of individual birds of each species (birds hr-1 day-1), corrected for observer effort
ii.	chronology	3	full day	daily hour of maximum species abundance, relatively scaled to sunrise
	chronology	4	dawn flock	time of peak value of a LOESS regression fit to dawn flock abundance, rescaled 0-1
iii.	functional roles	5	pioneer	tabulated occurrences where each species served in the pioneering dawn "dance" sortie
	functional roles	6	sentinel	tabulated occurrences each species sounded a warning alarm call that flushed the flock
iv.	interactions	7	displacement rate	number of times a species displaced another divided by the total agonistic interactions for that species
	interactions	8	interaction rate	total number of agonistic interactions with other species divided by the species' total daily individual abundance (component #2)
	interactions	9	interaction breadth	proportion of all species (*n* = 12) with which each species interacted

Table 1. Four categories of 9 total observed components of parrot sociality. Flock monitoring revealed 9 traits relevant for flock formation, participation, anti-predator vigilance, and status (see Figs 2-5). See Methods for more details.

Species Level Covariates

The ornithology collections of 10 institutions provided specimen access and morphometric data. These are the Carnegie Museum of Natural History, Museum of Comparative Zoology (Harvard University), University of Kansas Biodiversity Institute, Natural History Museum (Universidad Nacional Mayor de San Marcos, Perú), Florida Museum of Natural History (University of Florida), Burke Museum of Natural History and Culture (University of Washington), Bernice Pauahi Bishop

Museum, Museum of Vertebrate Zoology (University of California), and the North Carolina Museum of Natural Sciences. From study skins and spread wings, wing rules measured the wing chord (or closed wing length, L_w) and the span from the carpal joint to the first secondary feather's tip (S_1) of each wing. Vinyl measuring tapes recorded the curved and digital calipers the straight culmen and lower mandible lengths. Body mass (Brightsmith and Villalobos 2011) and brain volume (Schuck-Paim et al. 2008) is from published studies. Lacking the brain volume of *Brotogeris cyanoptera*, we averaged the values of 6 congeners. To visualize forms, we imaged spread wings and bills of focal species or their congeners on gridded surfaces.

To understand flight, we used L_w and S_1 to calculate the hand-wing index, total wing area index, and total wing load. The hand-wing index ("HWI") is correlated with dispersal ability (Claramunt et al. 2012, Claramunt and Wright 2017), an important trait in Amazonian forest birds (Van Houtan et al. 2007). Derived from L_w and S_1, HWI = $100*((L_w-S_1)/L_w)$. Total wing area is a key aerodynamic metric (Pennycuick 2008, Gagné et al. 2018b), summarized by an index ("TWAI") that equals $3S_1L_w$ (Claramunt and Wright 2017). Wing load is determined from reported body mass and median TWAI (Pennycuick 2008). Bill lengths captured factors relevant for dominance (Serpell 1982, Daily and Ehrlich 1994, Marcuk et al. 2020), we summed their straight and curved lengths. However, due to the increased possibility for error in measuring curved bills, we excluded those data. To describe cognitive aptitude we corrected for body size (Mace et al. 1981), taking the residuals from best fit power model of brain volume and body mass (Krebs and Davies 1993). With the taxonomic classifications of tribe, genus, and species (Schodde et al. 2013), these data are a suite of potential model covariates.

Random Forest Model Features

In line with previous ecological studies (Gagné et al. 2018a, Gagné et al. 2018b, Becker et al. 2019, Becker et al. 2020, Nicholson et al. 2023, Nicholson et al. 2024), we use Random Forest ("RF") algorithms to build nonlinear multiple regressions to predict parrot sociality. RF models are a machine learning tool with several advantages to linear least squares regression. RF models (i) are scalable to large datasets including categorical and continuous features, (ii) accommodate both nonlinearity and heteroscedasticity, (iii) present ensemble conclusions of decision trees made from randomized subsets of predictor and response data, and (iv) visualize the partial influence of multiple predictors on the model outcomes (Breiman 2001).

We trained an RF through resampling the dataset with 10-fold cross validation (repeated 5 times), set the number of model trees (*ntree* = 2000) and by tuning the number of available parameters at node splitting (*mtry*) for optimal performance. *K*-fold cross validation evaluates the model by splitting the data into k equally-sized sets; fitting it on the k-1 sets and testing it on the remaining held-out fold (Gareth et al. 2013). The routine loops for each k set, then summarizes model performance by calculating the ensemble average R^2 across all k tests (we repeated the entire process 5 times). We initially tuned and ran an RF using all available covariates (n = 10), but as many variables were correlated, we retuned and ran an RF using only 5 inputs without performance loss. These are: tribe, brain size, cumulative bill straight length, HWI, and wing load.

The R statistical language (RCoreTeam 2022) performed all analyses in macOS Sonoma 14.6.1 run on an 8-core M1 chip. The 'dplyr' and 'tidyr' libraries facilitated data wrangling (Wickham et al. 2023) and the 'caret' and 'randomForest' libraries (Liaw and Wiener 2002, Kuhn et al. 2020) trained, tuned, and fit RF regressions. The 'doParallel' library reduced computation times (Weston and Calaway 2022). The 'pdp' library generated partial dependence data (Greenwell 2017). A third-party repository (GitHub, `anonymized link`) contains data and code.

RESULTS 1049 words

We documented 16 species of Neotropical parrots (subfamily Arinae) at the TRC collpa (Fig. 1): 6 macaws, 5 parrots, 3 parakeets, and 2 parrotlets. Of macaws, we counted red-and-green (*Ara chloroptera*, "RGMA"), blue-and-yellow (*Ara ararauna*, "BYMA"), scarlet (*Ara macao*, "SCMA"), chestnut-fronted (*Ara severus*, "CFMA"), and red-bellied (*Orthopsittaca manilatus*, "RBMA"). The parrots are the mealy amazon (*Amazona farinosa*, "MEPA"), yellow-crowned amazon (*Amazona ochrocephala*, "YCPA"), blue-headed (*Pionus menstruus*, "BHPA"), white-bellied (*Pionites leucogaster*, "WBPA"), and orange-cheeked (*Pyrilia barrabandi*, "OCPA"). The parakeets are the white-eyed (*Psittacara leucophthalmus*, "WEPA"), dusky-headed (*Aratinga weddellii*, "DHPA"), and cobalt-winged (*B. cyanoptera*, "CWPA"). We observed dusky-billed (*Forpus modestus*) and Amazonian (*Nannopsiottaca dacchileae*) parrotlets at the collpa but only in monospecific flocks, after dawn. One additional macaw—blue headed (*Primolius couloni*)—was more furtive and occasionally seen perched in the trees above the feeding flocks. We consider neither *F. modestus*, *N. dacchileae*, nor *P. couloni* further. With the available technology (see Methods), the small macaws—RBMA and CFMA—evaded distinction while foraging and we lumped all their data as "GRMA." We further analyze 11 species and 1 species complex (GRMA).

Above and on the collpa, we observed various parrot group formations and activities (Fig. 1). The most pronounced activity occurred in mixed species aggregations immediately after dawn (Fig. 1b). Smaller—predominantly single species (Fig. 1c-d)—groups occurred sporadically throughout the day. All species foraging on the collpa also perched in the vegetation above it (Fig. 1e), where some would alarm birds eating clay below (Fig. 1f). Though up to 9 nine species and nearly 350 birds could be seen foraging on the collpa at one time, dawn flocks typically had peaks of richness of 6 species, abundance of 200 birds (Fig 1g-h) and activity 10-20 min. after flocks formed. Dawn flocks followed a consistent sequence of events and behavior (Fig. 2): sunrise, signaling calls, dance sortie of nuclear species, first landing of leading pioneers, steady sequence of arriving and leaving birds, followed by the end of feeding. Though dawn flocks might last > 80 min. (Fig. 2b), the median duration was 53 min. The dance sortie was typically brief (median = 3 min., Fig. 2b), and was tightly fixed to the timing of morning twilight (Fig. d-e). Over 99 days, researchers observed (Fig. 2f) 583 daylight hours biased toward dawn, with (Fig. 2g) a cumulative 749 observer hours spread over 79 discrete days.

Corrected for observer effort, species demonstrated distinct chronologies of activity, with most (*n* = 8) preferring dawn flocks (Fig. 3a). Assessed by total and peak abundance (Fig. 3a-b), 2 species (BYMA, SCMA) regularly joined both dawn and day flocks, while 2 others preferred day flocks (RGMA, CWPA). Whether ranked by (Fig. 3c) biomass or (Fig. 3d) individuals, BHPA and MEPA are the most abundant species recorded. We observed 50 BHPA and 30 MEPA individual birds hr^{-1} in each dawn flock. Most species (*n* = 8), however, have ≤ 5 birds hr^{-1} in the dawn flocks. Within the dawn flocks, species also demonstrated chronology preferences (Fig. 4). Though congeners, YCPA is the first species to arrive, while MEPA is second to last (Fig. 4a-b). The 3 earliest arriving species comprise the only pioneers (Fig. 4c) who lead dance sorties. This included both small macaws (CFMA, RBMA) that while easily differentiated in flight, were not distinguished by their dorsal plumage while foraging.

Flushes were common in dawn flocks (Fig. 5a, total = 1200, mean = 15.5), though most (999, 83.3%) were not attributed to a direct cause. For flushes that were (Fig. 5b), 163 (13.6%) were anthropogenic and 38 (3.2%) natural causes, with the leading known cause being passing tourist boats and tourists conspicuously viewing flocks from open trails above the collpa. (Birds of prey were common, however, with *Falco deiroleucus* and *Astur bicolor* actively attempting depredations of OCPA, WEPA, and DHPA.) Flushes preceded by sentinel alarms (Fig. 5c, n = 187) were unevenly distributed across 10 species. Four of the most common sentinels were late foragers in dawn flocks (Fig. 4a). Interspecific interactions revealed their frequency and status (Fig. 5d-e). BYMA, YCPA, and GRMA frequently interacted with many species, while SCMA, CWPA, and RGMA frequently interacted with few species (Fig. 5d). Status largely reflects body size (Fig. 5e). The largest species, RGMA, was uniquely dominant, with a win rate > 50% versus all other species. The smallest species, CWPA, was always subordinate (win rate = 0%).

We build a cumulative sociality score (Fig. 6a) from 9 individual metrics (Table 1). These metrics reflect flock abundance (Figs. 3), chronology (Figs 3-4), functional roles (Figs. 4-5), and interactions (Fig. 5). The cumulative metric appreciates species (e.g., BHPA, MEPA) that have high abundance, participate in dawn flocks, perform functional roles, and score high across 3 interaction metrics. The index relegates species (CWPA, WBPA) that do not express these traits. A weighted, non-parametric bootstrap sampling routine created 2000 sociality scores for each species (Fig. 6b) that retains the rankings of the raw score accumulation (Fig. 6a) while randomizing the raw data.

Museum specimens and published data reveal a range of morphometric indices relevant for status (Fig. 7a-c), flight (Fig. 7d-e), and cognition (Fig. 7f). Large macaws have the largest bills (Fig. 7c), where the small macaws and parakeets have the highest HWI values (Fig. 7d) suggesting greatest dispersal ability. The amazons have the highest wing loads (Fig. 7e). The fitted power model of brain size to body mass has an exponent of 0.70 (consistent with fitted relationships in birds (Krebs and Davies 1993)), revealing significant differences among species, even congeners (Fig. 7f).

The morphometric and taxonomic variables display a variety of pair-wise relationships to our sociality index (Fig. 8). Sociality increases as brain size (adjusted for body mass) decreases (Fig. 8a). Aerodynamic metrics have inconsistent relationships (Fig. 8b,e), bill size has a mid-domain peak (Fig. 8c) while the Androglossini tribe is above Arini (Fig. 8d). The trained, tuned, and optimized RF model performs well (R^2 = 0.959), ranking brain size ahead of HWI, wing load, bill length, and tribe (Fig. 8f). Model performance was insensitive both to removing correlated predictors and resampling procedures (see Methods). Partial dependence plots (Fig. 8g-j) display bivariate influences on model predictions (y^). The confluence of small brains, small HWIs, high wing loads and medium bills predict high sociality (Fig. 8g-h). Tribe has a negligible influence (Fig. 8j).

DISCUSSION 1400 words

While previous studies described geophagy in Neotropical parrots (Gilardi and Munn 1998, Gilardi et al. 1999, Brightsmith and Muñoz-Najar 2004, Brightsmith and Villalobos 2011), here we develop novel means to quantify various traits of cooperation and model their drivers with machine learning. Our main result is deriving a multivariate index of sociality and relating it to relative brain size. Fig. 8f shows that brain size is the strongest predictor of sociality, outperforming all factors. Directly interpreted, this suggests that species with smaller brains are the most active in mixed flocks, perhaps as they stand to gain the most from the advantages mixed societies provide. As observed in other animal collectives, such cooperation might increase foraging opportunities, foraging efficiency, and antipredator vigilance (Moynihan 1962, Ehrlich and Ehrlich 1973, Powell 1985, Terborgh 1990, Krebs and Davies 1993)—presumably increasing benefits and reducing risks to survival and fitness (Krebs and Davies 1993). An alternative explanation for our results derives from expensive tissue theory. As seen in mammals, frogs, and birds (Aiello and Wheeler 1995, Isler and van Schaik 2006, Liao et al. 2016), this suggests species with larger brains possess a comparative reduction in other metabolically demanding tissues, such as the gut. Here, small-brained parrots may have high sociality scores because they have correspondingly larger digestive tracts and, therefore, are most able to process soils and clays and extract their beneficial nutrients. As we cannot test this idea directly, it merits further examination in this context, as well as in mammal societies at mineral licks (Griffiths et al. 2020, Griffiths et al. 2023), and beyond.

The combination of pioneer, sentinel, and status data suggest reciprocal altruism functions between species. Foraging on the exposed collpa (Fig. 1a) poses major risks, as birds perch conspicuously in open areas with their vision restricted in foraging recesses (Fig. 1f). Flocks as a result are hyper-vigilant, frequently alarming and flushing to safety (Fig. 5a). Here an interesting tradeoff and separation of roles emerges. The 3 most vigilant sentinels (Fig. 5c: MEPA, SCMA, BYMA) are the most antagonistic, dominant (Fig. 5de), and among the latter species in the dawn flock sequence (Fig. 4ab). Nuclear species seldom serve as sentinels and the commonest sentinels are never in the leading dance sortie (Fig. 4c). As a result, sentinel species guard before feeding, sounding alarms from perches in vegetation above the collpa. When it is their turn to feed, sentinels land on the collpa where they often displace the feeding positions of pioneer species who previously established foraging perches. Though most single-species social groups have pioneer and sentinel roles (Clutton-Brock et al. 1999), here the roles are split between species. Other mixed-species bird flocks also split such roles between species, but in those groups the roles occur while all species forage simultaneously (Moynihan 1962, Munn and Terborgh 1979, Powell 1985, Terborgh et al. 1990, Hart and Freed 2003, Van Houtan et al. 2006). In this parrot society, the roles appear characteristically sequenced in time. Dominant, highly interactive sentinels like MEPA might delay foraging by > 20 min after subordinate pioneers like BHPA.

Congeners that shared many morphological traits also had distinct behaviors. The only Amazon parrots, MEPA and YCPA, have highly similar body size, bill, wing, and brain metrics (Fig. 7). Ultimately, these are the top 2 ranked species in the sociality index (Fig. 6), but they arrive there via different means. YCPA is a core nuclear species that was most frequent in the nuclear dance sorties (Fig. 4) where MEPA is a late arriving species in the dawn flock (Fig. 4a) and the most common sentinel (Fig. 5c). Our observations suggest their participation in foraging assemblages is almost mutually exclusive. Furthermore, the 3 large *Ara* macaws also have similar morphometrics (Fig. 7), are key sentinels (Fig. 5c) and are dominant over other species (Fig. 5e). However, RGMA rarely join dawn flocks, where BYMA and SCMA prefer them (Fig. 3a). Interestingly, BYMA has a noticeably smaller brain than either RGMA or SCMA (Fig. 7f) which may contribute to its higher sociality score (Fig. 6). Differences in the social preferences among closely related congeners in such mixed societies deserves more attention.

Future inquiries will improve on the present analysis. In all respects, ultra-high-definition digital imagery and video will advance the efficiency, ability, and precision of monitoring. This will help resolve the identification of cryptic (e.g., GRMA) and uncommon (*N. dacchileae*, *P. couloni*) species, attribution of flock threats and sentinel alarms (Fig. 5bc), reveal additional fine-scale interactions between species (Fig. 5de), and additional behaviors within species groups, such as nested or multiple hierarchal tiers (Papageorgiou et al. 2019, Camerlenghi et al. 2022) or mate selection. Combined with machine learning, such improved technology may also document the patterns, syntax, and significance of vocalizations. New estimations of total bird wing area (Fu 2022) may further assess flight performance, but require wingspans which are not measured from folded-wing study skins. Capture, marking, and biotelemetry present significant logistical challenges but would yield unprecedented insights into individual movement and habitat use. (Photographic identification is a potential non-invasive, alternative technique (Núñez-López et al. 2021).) In combination with biotelemetry and monitoring, feather ‘omics using bulk or compound-specific stable isotope analysis (Gagné et al. 2018b, Van Houtan et al. *in press*) would provide important diagnostic data on diet and trophic status. Replicating the present monitoring and analytical protocols in other locations, seasons, and over longer time periods is of value. Together, these methods may help assess the significance and selective pressures for cooperation and organization in dawn and day flocks of parrots foraging at mineral licks. Lastly, as they tend to range widely and more frequently encounter human hazards (Woodroffe and Ginsberg 1998, Van Houtan et al. 2007, Laurance et al. 2011), social species may become more prone to local extinction. Future attention should be given to the relationship between sociality and population status in these parrots, especially outside of protected areas.

As unsupervised statistical procedures have the potential of spurious correlations and overfitting (Gareth et al. 2013), our final model reduced the number of variables, averaged results from a large number of trees, and deployed cross-validation. The resulting RF avoids bias and is curated to the smallest set of taxonomic and morphometric predictors with directly relevant mechanisms. Bill size was the only unadjusted variable for body size as it is a leading predictor of parrot aggression (Serpell 1982, Marcuk et al. 2020). We optimized model performance by tuning the *mtry* hyperparameter from a possible range of values of 1:5. Factor rankings were insensitive to tuning, but larger *mtry* values skewed ranks. Though our analysis is a trait-based approach (Debastiani et al. 2021), it is constrained within the subfamily Arinae. Within this taxon, it remains possible that the data are phylogenetically structured (Felsenstein 1985). While this does not violate decision-tree-based model assumptions (as it does for LLS regressions (Bielby et al. 2010)), we took several measures to identify potential artifacts. First, out of 10 predictors, species and genus were the 2 poorest performing predictors in our initial RF model (14% and 2% relative ΔMSE, respectively). Second, in our final RF, the only remaining taxonomic variable again performed poorest (tribe: 3% relative ΔMSE, see Fig. 8f). Third, most of the remaining predictors (brain size, HWI, wing load) in the final model were corrected for the broad taxonomic influence of body size. Finally, we ran 2 *post hoc* RFs with the data split by tribe. In each single-tribe RF, brain size was ranked highly (Arini: 100% relative ΔMSE, Androglossini: 94% relative ΔMSE).

This study provides a comprehensive framework for describing the abundance and behavior of mixed societies of parrots, providing further evidence that birds are a compelling taxon for studying animal collectives (Gonzalez 2019, Farine 2022). We observed distinct patterns of the abundance and chronology of flock participation for 12 parrot species (Figs. 1-4). Beyond basic membership, species displayed canonical functions as nuclear and sentinel species (Figs. 4-5). Agonistic interactions (Fig. 5) revealed a dominance hierarchy, with several pioneer species being subordinate and sentinels dominant: partitioning and delaying the sequenced foraging of sentinels. Our multivariate index of sociality derived from these data was best explained by brain size (Figs. 6-8), providing a basis for future studies to examine further the physiological benefits of geophagy and the potential roles of cognition, gut processing, flight performance, or other species traits, as well as any broader relationship between relative brain size and cooperation in mixed animal societies.

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AUTHOR CONTRIBUTIONS: KV designed the study, raised research support, administered the project, contributed data, entered and analyzed the data, wrote the code, performed the analysis, created the figures, and wrote the manuscript. JR, HV and OG contributed data and reviewed the manuscript.

DATA AVAILABILITY: All datasets and code used here are available at a third-party repository (GitHub, bit.ly/3qW45Md). *This repo is currently private and will become public when the manuscript is accepted for publication.*

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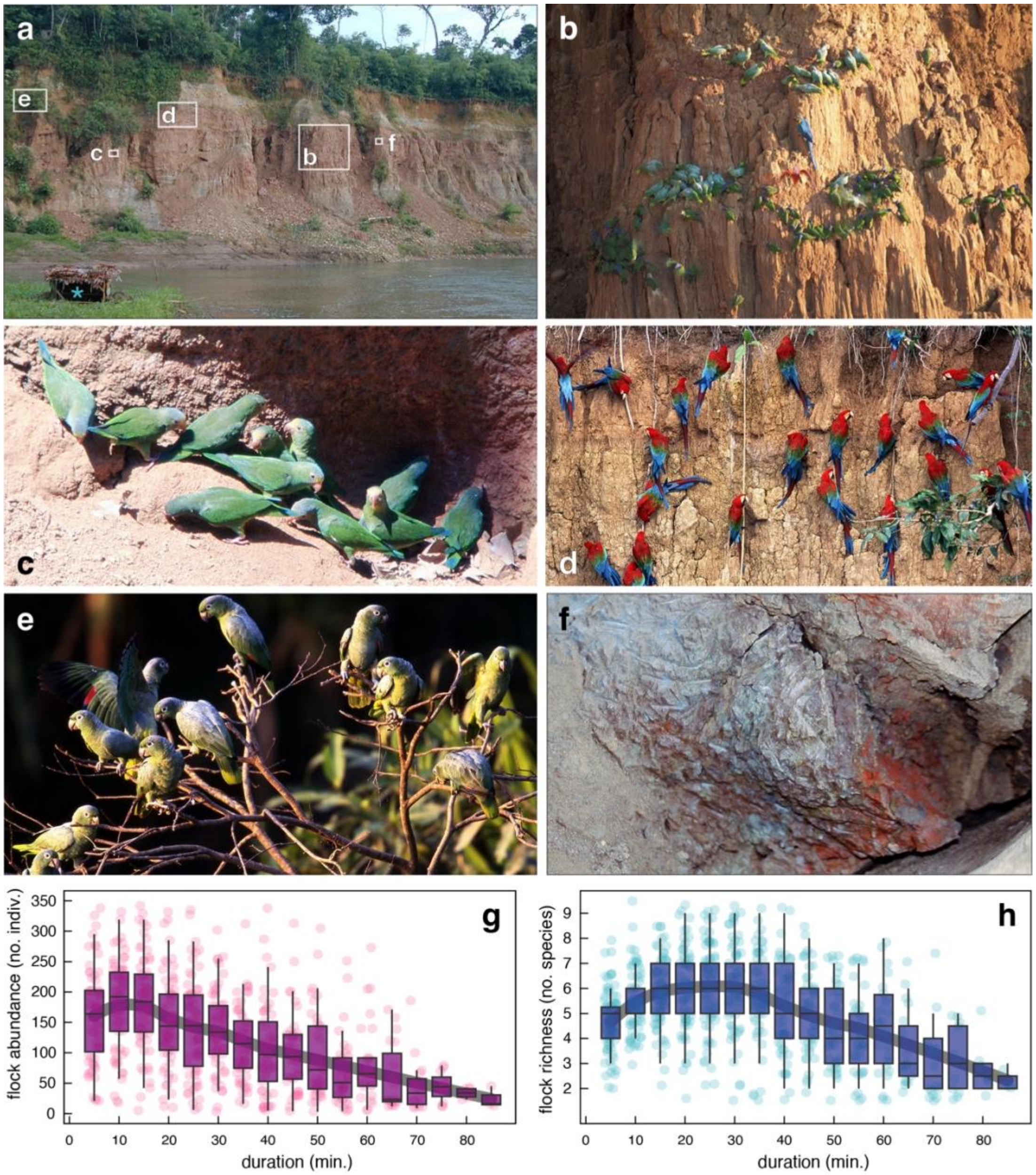

Figure 1. Parrots feeding on a clay cliff in Tambopata, Perú. (a) A ~100m wide transect of exposed dirt revealing stratigraphic clay layers below *várzea* forest. Labelled cliff regions correspond to figure panels, with the Tambopata river and observer blind (denoted by *) in the foreground. (b) Mixed-species foraging aggregation that gathers near dawn, here contains 6 species: mealy amazon (*Amazona farinosa*), blue-headed parrot (*Pionus menstruus*), orange-cheeked parrot (*Pyrilia barrabandi*), chestnut-fronted macaw (*Ara severus*), blue-and-yellow macaw (*Ara ararauna*), and scarlet macaw (*Ara macao*). (c) Cobalt-winged parakeets (*Brotogeris cyanopterza*) and (d) red-and-green macaws (*Ara chloroptera*) forage throughout the day, often in single species groups. (e) Mealy amazons perched in a nearby tree serving as sentinels, sounding alarm calls to warn cliff-foraging birds of threats. (f) Bill markings on exposed cliff surface reveal mineral-rich clays. (g-h) Raw data (circles) and summaries (boxplots) of abundance and species richness of birds foraging in morning flocks (*n* = 79) from June-September 1999. Thick line is a locally weighted regression ("loess"), points are slightly jittered. Though foraging bouts may last over 80 minutes, peak abundance and richness occurs 10 and 20-25 minutes, respectively, after flock foraging begins. Images (c-e) provided by E. Hummel and used with permission, all other images from the authors.

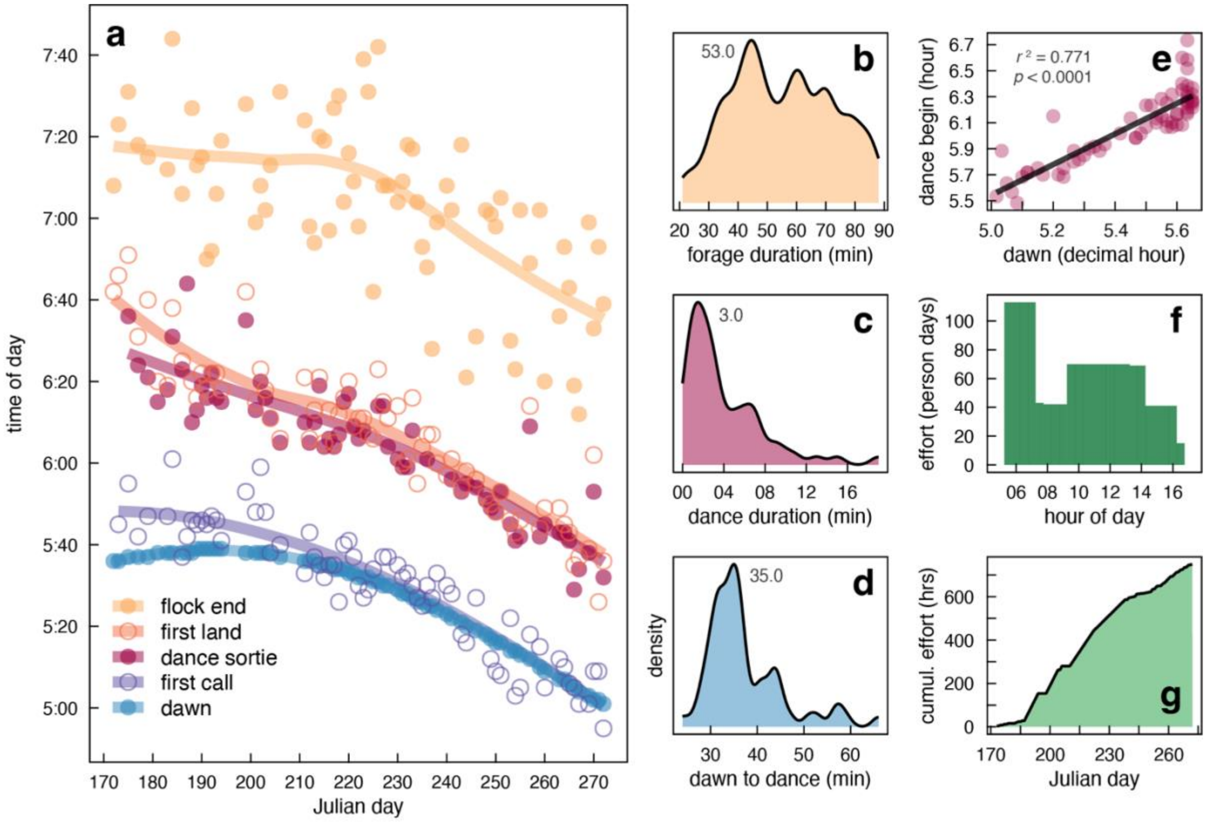

Figure 2. Dawn flocks of clay-foraging parrots have a characteristic behavioral sequence. (a) Raw observations (circles) and loess models (lines) document the chronology of dawn, first vocalization, multispecies sorties that encircle the cliff face searching for a landing site ("dance sortie"), first group landing, and foraging end. Density plots show the median duration of (b) morning flocks is 53 minutes and (c) dance flights is 3 minutes. The (d) median time elapsed from sunrise to the dance is 35 minutes, and (e) a linear model of dawn hour to dance hour suggests a causal relationship. Over a span of 99 days, observers monitored the clay cliff (f) from dawn until late afternoon, observing 583 daylight hours, with (g) 783 observer hours over 79 discrete days.

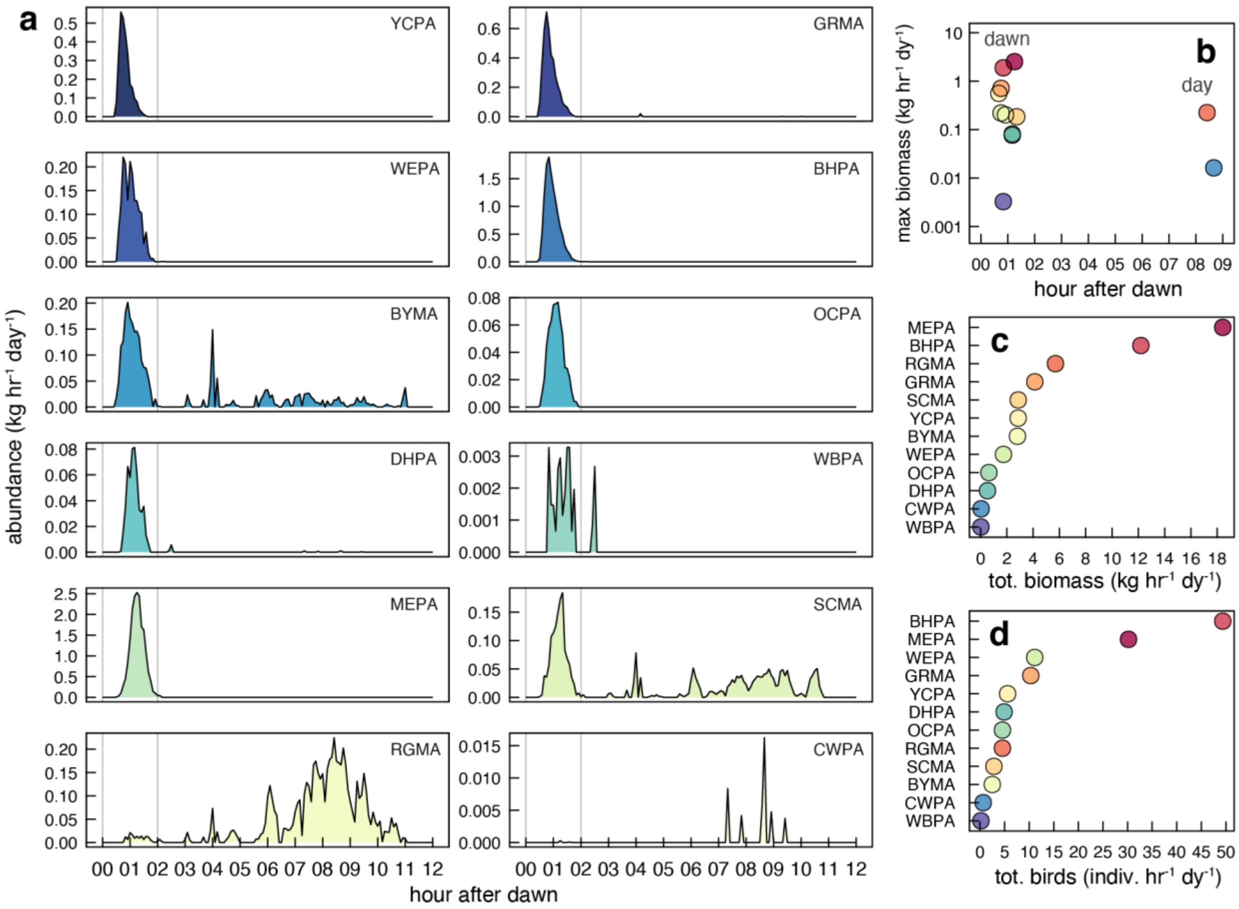

Figure 3. Observed species abundance of dawn and day parrot flocks. (a-b) Corrected for effort, species abundances map their chronology and peak occurrence. Uncommon in dawn flocks, (b) cobalt-winged parakeets (CWPA) and red-and-green macaws (RGMA) preferentially forage ~ 7-9 hours after dawn. As the entire species set represents individuals with biomass of 70–1,200 g, we express total abundance in (c) biomass, and (d) number of individuals. Mealy amazon (MEPA) and blue-headed parrot (BHPA) top both lists. Panels in (a) are sorted chronologically by maximum species abundance, vertical grey lines mark the 2 hours after dawn. Filled-circle color symbology retained in (b-d). Due to the technological difficulty of distinguishing foraging small macaws on the cliff, “GRMA” combines red-bellied macaw (*Orthopsittaca manilatus*) and chestnut-fronted macaw (*Ara severus*) observations. Methods define all four-letter species codes.

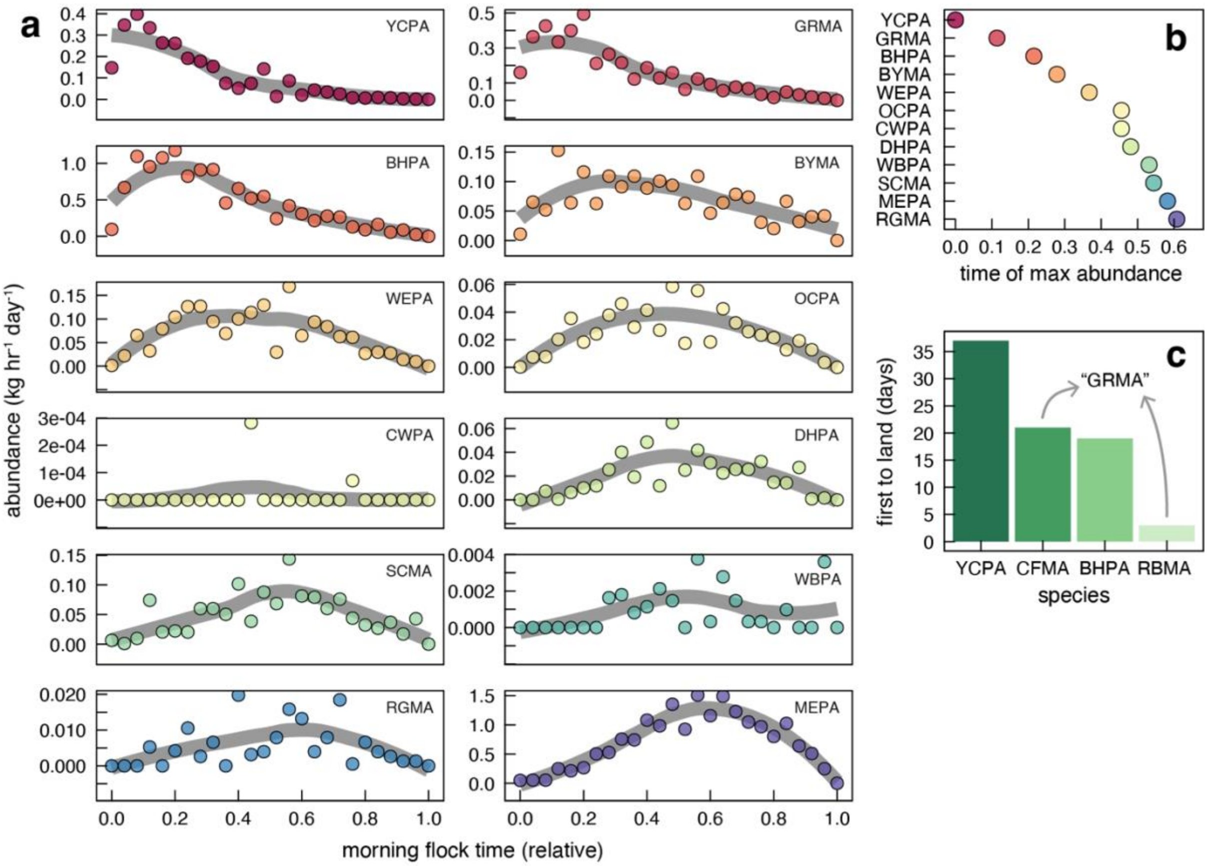

Figure 4. Dawn flock sequencing and pioneer species. (a-b) When considering dawn flocks alone, species show distinct early, middle, and late arrival tendencies. For each species in (a), grey line is a loess model of abundance, whose (b) maximum value captures sequence differences. Though congeners and both dawn-focused species, the yellow-crowned (YCPA) amazon is the first to arrive while the mealy amazon is last. (c) Observed pioneer species from dance sorties are first to land and therefore establish the dawn foraging events. Both small macaw species have significant pioneer roles.

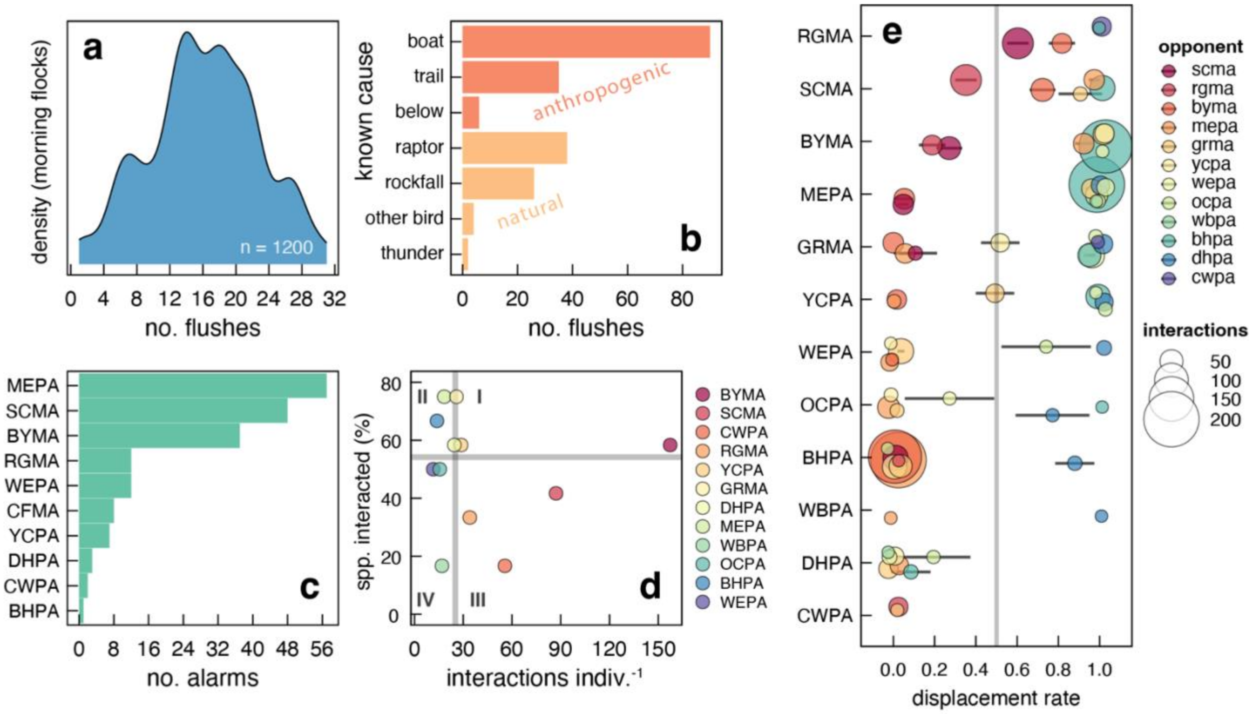

Figure 5. Flushes, sentinel alarms, and species interactions in flocks. (a) Flush events, where >50% of clay-foraging birds abruptly disperse from their cliff perches, are common and have (b) various causes. All anthropogenic known causes are ecotourism related: boats ferrying guests to view the dawn flocks, hikers exposed on the trails above the cliff, and unconcealed tourists on the observation beaches below. Flushes events are often preceded by alarm calls from sentinel birds perched in trees above the cliff. (c) Though 10 species served as sentinels, the most vigilant species (MEPA, SCMA) arrive late to forage in dawn flocks (Fig. 4ab). We observed 1,268 agonistic interactions between species, where an individual from one species displaces the foraging perch of another. Grey lines in (d) are the median values of each axis, defining four quadrants of interactions: (I) frequent with many species, (II) few with many species, (III) frequent with few species, and (IV) few with few species (see Methods). (e) Large-bodied macaws and amazons are dominant, winning most interactions. Vertical grey line is the 50% displacement (win) rate, circle size is the number of interactions, error bar is standard error.

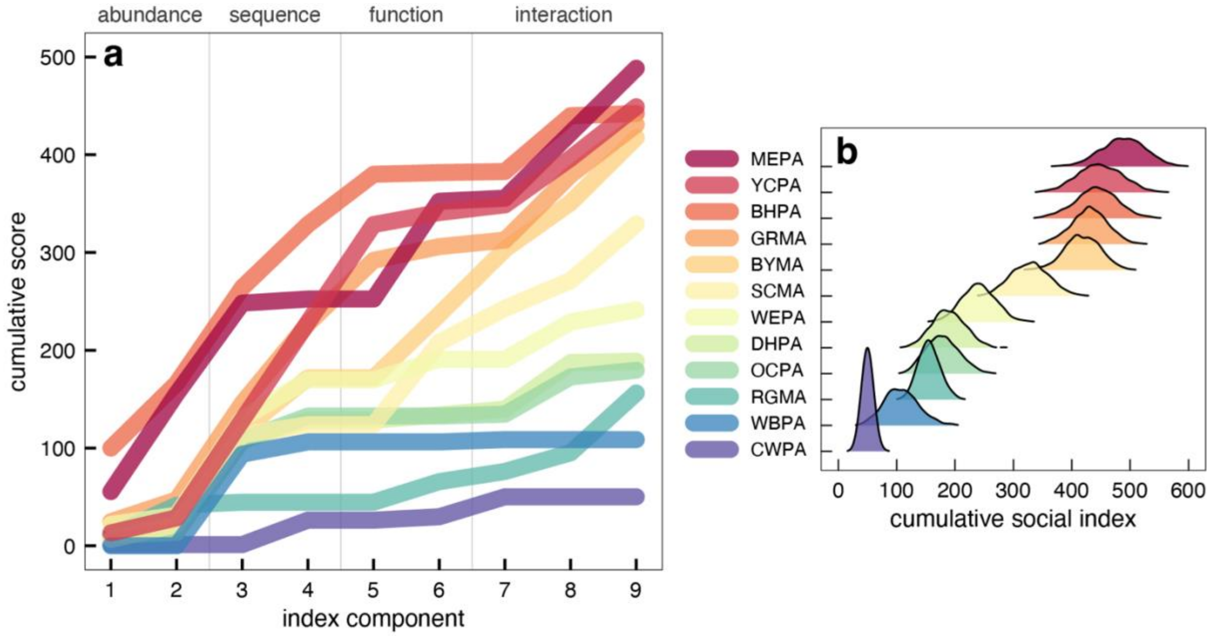

Figure 6. Multivariate index derives and ranks parrot sociality. (a) Our sociality index accumulates values from nine independent measured components (each rescaled to 0-100) across four distinct categories to capture a full suite of metrics that are important for mixed-species flocks of foraging parrots. These are abundance (1 = individuals, Fig. 3d; 2 = biomass, Fig. 3c), sequence (3 = peak biomass hour, Fig. 3b; 4 = dawn flock order, Fig. 4b), function (5 = first landing, Fig. 4c; 6 = alarming sentinels, Fig. 5c), and interaction (7 = species interacted, Fig. 5d; 8 = interaction rate, Fig. 5d; 9 = displacement rate, Fig. 5e). (b) Using random sampling with replacement and equal category weighting, nonparametric bootstrapping generated a cumulative social index, replicated 2,000 times for each species (see Methods). The output (b) provides a robust convergence of species index values and rank order. Color legend shared in both panels.

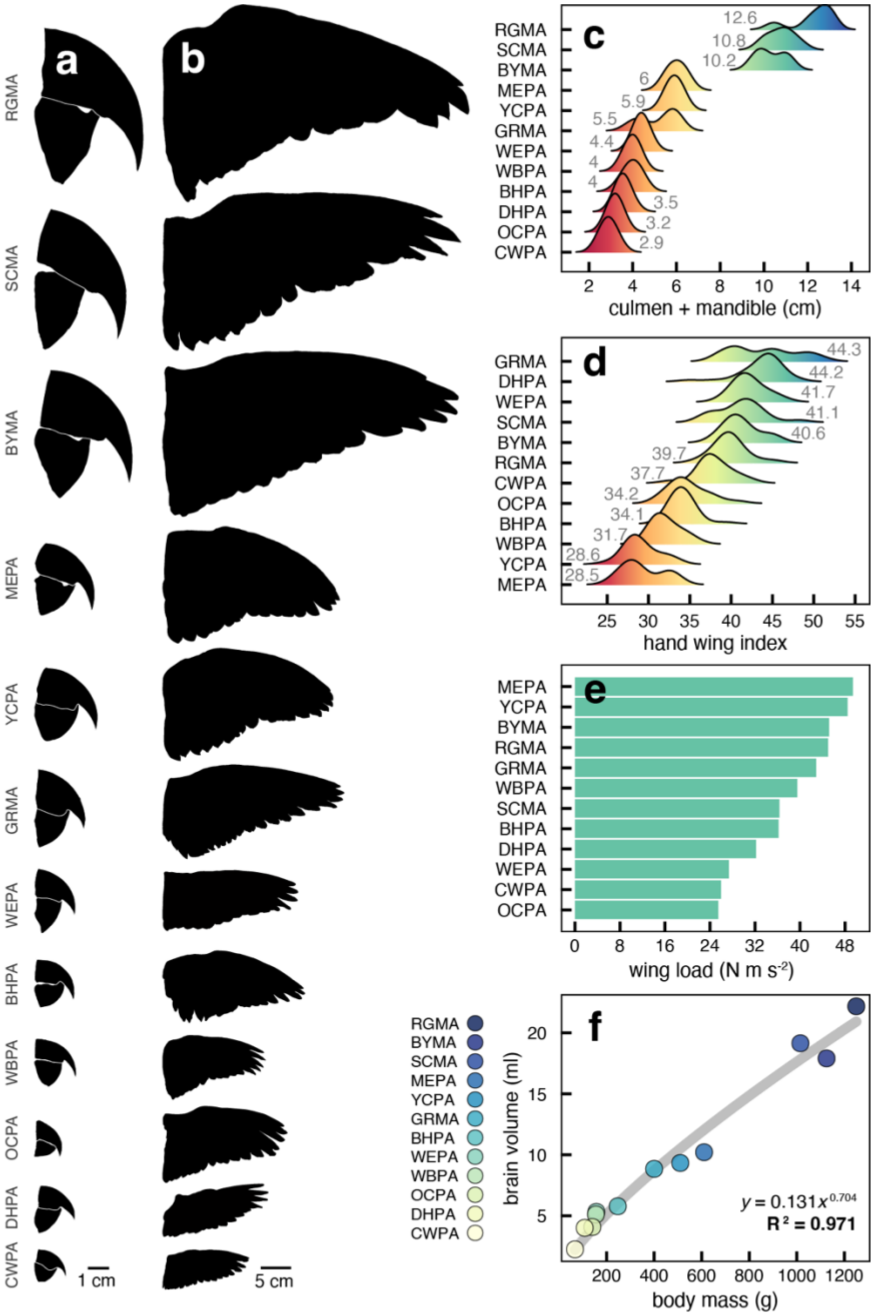

Figure 7. Relevant morphological metrics comprise potential predictors of sociality. Silhouette tracings of species (a) bills and (b) wings demonstrate morphometric patterns. (d) Aggregate culmen and mandible lengths increase with dominance (see Fig. 5e), (c) hand wing indices predict dispersal ability (Claramunt and Wright 2017), and (e) wing loads affect flight efficiency. Listed grey values in (c-d) are sample medians. (f) Residuals from best fit of the power model of brain volume to body mass (Krebs and Davies 1993) compare brain sizes.

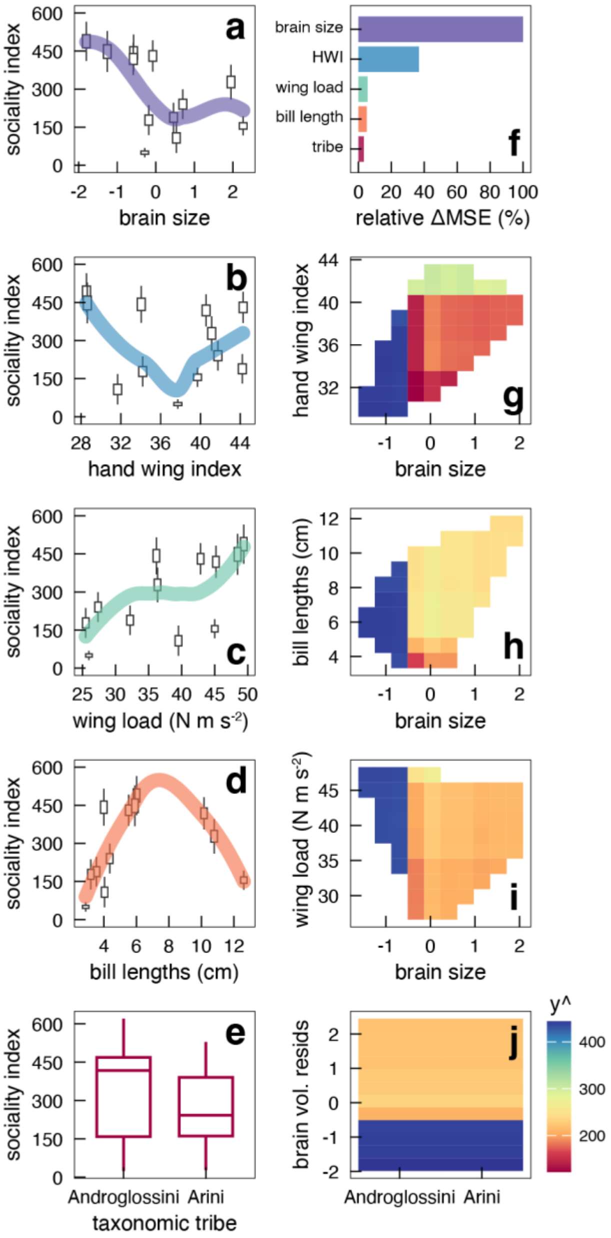

Figure 8. Small brain size and small hand wing indices drive sociality. (a-e) Raw pairwise comparisons of sociality against five covariates show broad pre-model variable relationships. (a-d) Trends are loess regressions; boxplots describe species indices from Fig. 6b. (f) Pre-trained and optimized RF models (*ntree* = 2000, *mtry* = 5) indicate brain size and hand wing index are the primary model drivers ($R^2 = 0.96$), bar colors correspond to (a-e) symbology. (g-j) Partial dependency plots display RF outputs, highlighting variable interaction in modeled predictions of sociality (*y*^), and the persistent importance of brain size.