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Behavioral Observations of Free-Living Scarlet Macaws (*Ara macao*) in Costa Rica, to Inform Ex Situ Management

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Abstract: The scarlet macaw (*Ara macao*) is a charismatic species that is native to Central and South America and commonly housed in captivity. Gaps in knowledge about these birds' behavioral ecology in the wild hinders both in situ and ex situ management and conservation efforts for this species. We conducted seventeen days of observations of free-living scarlet macaws in two locations in Costa Rica, in February 2022, with the aims of (1) advancing our knowledge of this species' natural behavioral ecology, and (2) generating data for comparison with captive macaws to help to inform their ex situ management (e.g., enclosure design and enrichment). Routes were walked within two locations—Bosque Escondido (BE), release area for captive-bred reintroduced individuals and no extant wild population, and Punta Leona (PL), an area of natural habitat within a resort inhabited by wild scarlet macaws—and focal interval sampling of multiple scarlet macaws in a group was used to record behavior and space use. The macaws at both locations were generally active, spent most of their time high in the tree canopy, relied on climbing to move within it, and used a wide variety of supports. The macaws at PL spent significantly more time feeding and locomoting, and less time perching, than those at BE, possibly due to differences in resource availability, rearing conditions, and age. Furthermore, the wild scarlet macaws at PL exhibited a variety of foraging strategies to acquire and manipulate food items within the tree canopy, including frequent use of their feet during manipulation. Despite limitations caused by a small sample size, a short period of observations, and differences between the two populations observed, this study provides insights into the behavioral ecology of scarlet macaws in the wild, which can be used for behavioral assessments of captive macaws while informing their ex situ management, with applications to animal welfare and captive breeding programs.

Keywords: behavioral ecology; ex situ conservation; in situ research; reintroduction; scarlet macaw

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1. Introduction

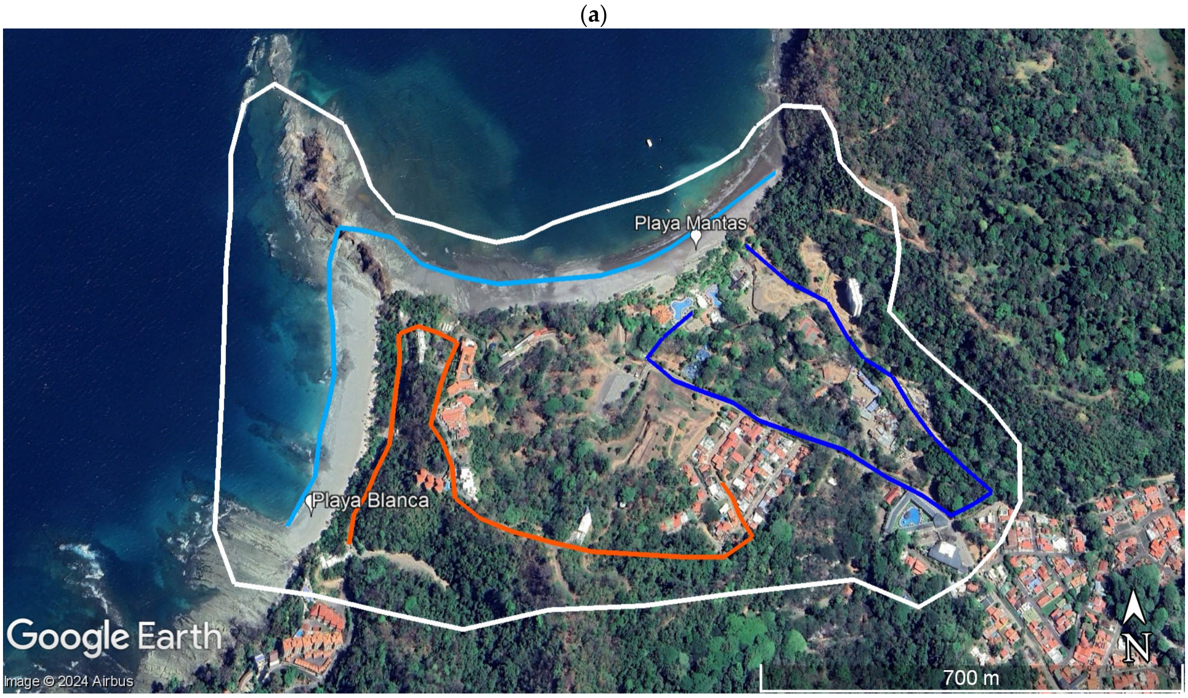
Animal behavior research can be a vital tool in conservation. In in situ contexts (i.e., within the species' historical range), it facilitates the assessment of animal responses to human impacts and changes in the environment, while also informing the implementation and management of conservation actions [1]. In ex situ contexts (i.e., outside natural habitat), it improves captive breeding programs, by facilitating the preparation of captive-bred animals for release into the wild (e.g., assessing whether they are displaying the necessary wild-type behaviors for survival and adaptation to the new environment, and informing changes in captive management to enable those behaviors), and the post-release monitoring of their adaptation to the wild [2]. Assessing animal behavior is therefore a key step in addressing some of the main challenges of captive breeding and reintroduction programs: with the loss of natural/wild-type behaviors [3] and morphological alterations [4] animals can experience in captivity, their preparedness to survive in the wild is reduced [5].

Behavior is also one of the indicators often used in animal welfare assessments, alongside others such as physical health and physiology [6], and can therefore be used to assess and improve the husbandry and welfare of animals under human care [2]. Captive animals can benefit from research on their wild counterparts [7], as basing the ex situ management of a species on scientific evidence, generated from research on its natural history, rather than traditional practice, has been found to improve animal husbandry and welfare [8]. As the natural/wild conditions in which species live influence the evolution of their behavioral needs and coping mechanisms [9], allowing captive animals to express those behaviors in captivity can be rewarding to the animals and therefore beneficial to their welfare [10]. On the other hand, wild animals also experience sub-optimal welfare, and replicating natural behaviors in captivity that are associated with aversive experiences in the wild (e.g., avoiding predation, competition for resources) may be detrimental to the welfare of the animal [10]. Although not all natural behaviors are associated with positive welfare, and the relationship between each behavior and welfare needs consideration, knowledge of the natural environment and behavioral ecology can still be useful to inform ex situ husbandry [10,11]. Therefore, gaps in that knowledge hinder both ex situ conservation efforts and animal welfare.

The scarlet macaw (*Ara macao*) is a Neotropical parrot species, with a range that includes areas in Central and South America [12]. Although not globally threatened (Least Concern in the International Union for the Conservation of Nature [IUCN] Red List of threatened species), their numbers are declining [12]. They are popular among humans, as one of the most common bird species in the pet trade [13], and with a significance to human culture that dates to the 10th century, when they were acquired as symbols of social status [14]. They are also common in zoos all over the world, with over 1400 individuals recorded in ZIMS (Zoological Management Information System), housed in over 200 institutions across six regions [15]. Despite this popularity, research on the behavioral ecology of this species is still limited, with published in situ research focusing on feeding observations [16], nesting and parental behaviors [17,18], post-fledging movements [19], migratory patterns [20], and geophagy [21]. Other studies have also investigated the behavior of released captive-bred individuals, with the aim of assessing their adaptation to the natural environment [22,23]. Furthermore, some of the existing behavioral research on wild macaws (genus *Ara*) relies on qualitative observations alone (e.g., descriptions of food manipulation [16,24]) which, although useful to inform ex situ management, are of limited use for in situ–ex situ comparative studies. Data on time budgets of free-living scarlet macaws are limited, and only available for captive-bred released animals [22] and juveniles up to 11 weeks old [19] while quantitative data on behaviors such as foot use during feeding, type of support use, frequency of different types of locomotion and social behaviors, proximity to conspecifics, and space use were not found. These data collected from wild individuals can be used for comparison with their captive counterparts and determine whether the latter exhibit similar frequencies of wild-type behaviors. Even though these comparisons have limitations, due to the different needs of captive and wild animals [10], they can be helpful in conservation breeding programs (e.g., when evaluating whether a captive animal is suitable for reintroduction into the wild [22], one of the challenges of ex situ conservation [5]), and can also be useful alongside other indicators (e.g., health and affective states), as part of animal welfare assessments [11].

The scarlet macaw population in Central America is less than 4000 individuals, with 2000 estimated to remain in Costa Rica [25]. The Central Pacific Conservation Area, located in western central Costa Rica, constitutes over 500,000 ha of varied habitat, and it is inhabited by 83.6% of the 892 bird species identified in the country [26]. Despite having one of the two viable scarlet macaw populations in Costa Rica (the other is located further south at Osa Peninsula; Figure 1a), surveys from the early 1990s showed a declining population in that region, which could have led to local extinction if there had been no intervention [27]. Collaborative conservation efforts, which were set up in 1994 and included anti-poaching measures, placing artificial nests, natural nest protection, economic incentives to local communities, and environmental education, were successful at stabilizing the population [27]. The Hotel y Club Punta Leona, a resort and tourist attraction within the Central Pacific Conservation Area in Puntarenas (Figure 1a), and one of the main partners in the conservation efforts for the scarlet macaw in the region, protects over 100 ha of primary and secondary forest, beaches and trees within developed areas [28]. Between 1995 and 2018, 15 natural nests were found within that area and artificial nests have also been placed there and occupied by scarlet macaws [28].

(**a**)



(**b**)

Figure 1. (**a**) Locations of Bosque Escondido (in Nicoya Peninsula) and Hotel y Club Punta Leona (within Central Pacific Conservation Area), where data collection took place, as well as Barra Honda and Palo Verde National Parks, and Osa Peninsula are indicated for reference. (**b**) Detail of Hotel y Club Punta Leona. Observations took place within the area bounded by the white line, which included two beaches. The colored lines represent the three routes walked during data collection. Map by Google Earth Pro [29].

Only small and isolated scarlet macaw groups remain in the Nicoya Peninsula (northwest of Costa Rica; Figure 1a). Surveys conducted in 2016–2017 found only 14 individuals and seven nests, distributed across 800 km^2 in two national parks (Barra Honda National Park and Palo Verde National Park; Figure 1a) [30]. In 2016, the Rescate Wildlife Rescue Centre, a non-profit wildlife rehabilitation organization, started a scarlet macaw reintroduction project south of those national parks, at their Bosque Escondido release site (Figure 1a), in an 1800-acre dry tropical forest [31]. Their goal is to re-establish a population of this species in the area, by releasing 300 captive-bred individuals over 15 years [32].

The aims of this study were to (1) provide a basic behavioral description of the behavior of free-living scarlet macaws at two locations in Costa Rica (a wild population in Punta Leona and a reintroduced population in Bosque Escondido); (2) use those behavioral observations to create broad activity budgets, and also quantify space use, manipulation and foot use, structural support characteristics, and social proximity; and (3) gather evidence to inform ex situ management and husbandry of this taxon.

2. Materials and Methods

2.1. Locations and Populations

Data were collected in February 2022, during the dry season [33], at two sites in Costa Rica: (1) Rescate Wildlife Rescue Center's Bosque Escondido release site, near Pilas de Canjel, Nicoya Peninsula (Figure 1a), and (2) Hotel y Club Punta Leona, in Puntarenas (Figure 1a), within an area that included two beaches, forest, and areas with buildings (Figure 1b).

The scarlet macaws at the Bosque Escondido (hereafter, BE) site were part of a reintroduction program started in 2016. There were no remaining scarlet macaws at that site prior to 2016, so it is most likely that the scarlet macaws observed were captive-bred, and no older than seven years old, as they were approximately one year old at the time of their release [31]. Due to the young age of the released macaws, it is likely that the birds observed in this study were all captive-bred and not the offspring of released macaws. Furthermore, breeding had not been recorded by the team that monitors the released population (M. Gonzaléz, pers comm., 2022). In contrast, the scarlet macaws observed at Punta Leona (hereafter, PL) were part of one of the two remaining viable populations of scarlet macaws in Costa Rica. The observations in this location were most likely of wild scarlet macaws of various ages, as this population has been monitored since 1995 as part of an in situ conservation management program, and it is unlikely that captive-bred individuals released in the Nicoya Peninsula traveled to this area [28].

2.2. Behavioral Data Collection

Three routes of approximately 1500 m length were chosen from the paths available at each location (i.e., paths already used by the visitors and staff of the resort at PL, and by the staff of the reintroduction program at BE). At PL, one route crossed two beaches (light blue line, Figure 1b), one crossed an area of rainforest interspersed with holiday houses (orange line; Figure 1b), and the third one crossed an area with holiday and staff houses, a swimming pool, and bar within patches of rainforest (dark blue line; Figure 1b). The detailed location of the routes at BE could not be shared, for protection of the released animals, but all routes were within areas of secondary dry tropical forest, and one of them included the artificial feeders provided for supplementary feeding of the released macaws. The routes were walked between 06:00 and 16:00 hrs at BE, and 06:00 to 18:00 hrs at PL (Central Standard Time). Data collection finished earlier in the day at BE due to safety reasons, to give the observer time to return to the accommodation before dark, which was not necessary at PL. The order of the routes was selected randomly, and the same route was not walked in successive periods. While walking the routes, if scarlet macaws were found within a visual range, they were sampled until they moved out of sight, with the walk then proceeding until more individuals were found. When the observer identified an individual or group that had already been sampled during a walk, the walk proceeded and that individual or group were not sampled again. However, it is possible that re-sampling of individuals during a walk occurred if the observer failed to identify an individual that had already been sampled.

Focal interval sampling of individuals was conducted, with random selection of individual macaws in each observation interval when more than one was present (further explained in Section 2.2.1). Focusing on one individual in each observation interval allowed for accurate observations and collection of detailed behavioral data. Data were collected using the ZooMonitor mobile application [34], in 10 min sessions and 40 s intervals. Breaks of two minutes were taken between subsequent sessions. The weather conditions (cloudy, partially cloudy, clear/sunny, rain) and average temperature (determined from Apple iPhone's weather mobile application) were recorded at the start of each 10 min session. The sampling method was adapted from a study on captive scarlet macaws that involved over 400 h of behavioral observations [35]. After three hours of practice behavioral observations of free-living scarlet macaws, our sample protocol was refined to reflect the challenges of in situ data collection. The 10 min sessions were considered suitable for use on the highly mobile free-living macaws, to reduce the number of interrupted sessions due to individuals moving out of sight. Furthermore, 40 s intervals were found to be the shortest interval that could be used (and therefore maximizing the amount of data collected in a session; i.e., 15 intervals in a 10 min session) while allowing enough time to accurately select a random individual for sampling in each observation interval.

Individual macaws were sampled more than once, which was necessary to increase the sample size of behavioral data collected under the time restrictions of the study. Although auto-correlated data were collected as a result of repeated observations on the same individuals, it allowed for more detailed behavioral data to be collected [36]. To reduce issues of over-sampling individuals and auto-correlation, when only one macaw or pair were visible, they were sampled for up to 30 min (three 10 min sessions), while groups of 3–4 were sampled for up to an hour (six 10 min sessions). Groups with more than four individuals had no time limits. If no individuals remained visible for sampling, the session was terminated earlier, otherwise it continued with the new individuals that arrived. The routes in each location were randomly selected and walked at least twice a day (once in the morning and once in the afternoon); although at PL, it was often possible to carry out multiple daily walks to ensure the limited locations available for observations were sampled at different times of the day.

The released scarlet macaws at BE received supplementary feeding through artificial feeders hanging in the tree canopy on a pulley system. Feeders were replenished twice per day (once shortly after sunrise, and once between 15:30 and 17:00 hrs), by the local staff of the reintroduction program. They were fed a mixture of fruit and vegetables chopped in halves or quarters, nuts, and beans. No supplementary feeding occurred at PL, but some of the (occupied) artificial nests placed in the area, part of the in situ conservation management for the species, were within the area visited during our observation walks. Although the chance of observing scarlet macaws was higher in these areas, the group size-dependent time limits and the randomized route walks likely reduced the bias towards the individuals and/or behaviors associated with those areas.

2.2.1. Random Individual Selection in Group Sampling

Focal sampling of multiple individuals within a group was carried out by selecting a random individual in each observation interval, based on their position relative to other individuals, and using a pre-defined list of random numbers (Figure S1a) generated using Microsoft Excel (function "RANDBETWEEN"). The relative position of the individuals was used to select an individual, by counting heads left to right. For example, if the interval listed random number "3", the third individual from left to right was selected for sampling in that interval. When the heads of two individuals were in the same horizontal position, then the one higher in the tree was counted first. The number in the right column was used unless the number was greater than the number of visible individuals to be sampled.

For example, if there were four visible individuals for selection, and the right column had number "6", and left column had number "2", then the latter would be selected. When the numbers in both columns were greater than the number of visible individuals, then the individual furthest to the right was selected (see Supplementary Materials). When sampling fewer than three individuals, the lists were not used. When sampling two individuals, the individuals on the left and right were selected in uneven and even intervals, respectively. If only one individual was visible, that individual was sampled for up to 30 min or until it moved out of sight. However, a list was always ready for use in case more individuals joined the pair during a session, picking up from the interval they joined (e.g., if more scarlet macaws became visible on interval 4 of observations on a pair, then a list of random numbers would be used from the next full interval).

2.2.2. Ethograms of Behaviors of Scarlet Macaws

Three protocols were used for data collection: object manipulation, locomotion, and social behaviors, which were used on rotation for sampling. Our categorization of behaviors was based on ethograms that were created during a study on captive scarlet macaws [35] featuring contextual behaviors (Table 1).

Table 1. Ethogram of broad/contextual behaviors, and respective modifiers, of scarlet macaws. NA = not applicable as no modifiers for that behavior.

Category	Description	Modifier	Description
Out of sight	Individual obscured, no behavior can be identified.	NA	NA
Perching	Individual is standing in one position, completely immobile or showing head movements only. The individual may be alert, sleeping or resting but not engaged in any other behavior (except comfort behaviors: see modifiers).	None	The individual is immobile and not engaged in any other behavior.
		Unknown	The individual is immobile, but it is partially obscured, and it is unclear whether it is performing any of these behaviors.
		Stretching	Individual is stretching a part of the body while resting.
		Yawning	Mouth open widely while resting.
		Feather fluffing	Individual fluffs feathers and shakes body.
		Chewing (mouth movements)	Chewing movements while resting AND no object or food item can be seen in their bill.
		Wing flapping	Individual is flapping wings without changing location.
		Vocalizing	Individual is vocalizing while perching.

Table 1. *Cont.*

Category	Description	Modifier	Description
Self-maintenance	Individual is cleaning or tidying its own body.	Preening	Use part of the body (usually bill or head) to clean own feathers.
		Scratching	Using foot in a rapid movement to scratch part of the body.
		Foot Maintenance	Using mouth to gently manipulate own foot.
		Bathing	Feather fluffing, body shaking and head movements while immersed in water (e.g., in a puddle).
		Rain bathing	Feather fluffing, wings flapping and/or open while exposed to rain.
		Bill wiping	Wiping bill on a structure.
Feeding/drinking	Food/water search, manipulation, and consumption.	More detailed behavior collected when conducting "object manipulation" protocol.	
Geophagy	Soil and clay ingestion.	More detailed behavior collected when conducting "object manipulation" protocol.	
Object manipulation	Utilizing and interacting with a non-food object.	More detailed behavior collected when conducting "object manipulation" protocol.	
Social	Social interactions with other individuals.	More detailed behavior collected when conducting "social" protocol.	
Locomotion	Individual moving between locations.	More detailed behavior collected when conducting "locomotion" protocol.	

In addition, ethograms of specific feeding and object manipulation behaviors (Table 2), locomotion (Table 3) and support use (Table 4), and social behaviors and proximity (Table 5) were also created.

Table 2. Ethogram of object manipulation-specific behaviors, and respective modifiers, of scarlet macaws. * Multiple modifiers can be selected in that category.

Category	Description	Modifier	Description
Feeding	Food/water ingestion and/or manipulation.	Mouth (body parts used) *	Mouth is being used to manipulate the food/object but it is unclear whether both the bill and tongue are used or just one of them.
		Bill (body parts used) *	Bill is used to manipulate the food/object.
		Tongue (body parts used) *	Tongue is used to manipulate the food/object.
		Foot (body parts used) *	Foot is used to manipulate the food/object.

Table 2. *Cont.*

Category	Description	Modifier	Description
Object manipulation	Manipulating a non-food object.	Passive (level)	Searching for or holding an object or food item without actively manipulating it.
		Basic (level)	Basic manipulation that may include rotation with foot and/or soft biting, immediately followed by the destruction or ingestion of the food or object (e.g., biting a twig or leaf, biting off chunks of fruit).
		Intermediate (level)	May include persistent handling and/or gnawing of food or object items that require more extensive manipulation before destruction or ingestion (e.g., cracking seeds, peeling food item, gnawing on a perch).
		Advanced (level)	Advanced manipulation that may include extreme persistent handling and/or gnawing (e.g., cracking nuts), or manipulation that requires solving a cognitive challenge (e.g., tool use).
		Stationary (movement)	The individual's body stays in the same location while manipulating food or object.
		In motion (movement)	Individual's body changes location while manipulating the food or object.
Geophagy	Ingestion of earth or soil-like substrates.	Soil (type)	The individual is ingesting loose soil on the ground.
		Wall (type)	The individual is ingesting compacted earth from a wall (e.g., clay lick).

Table 3. Ethogram of locomotion-specific behaviors (Locomotion protocol), and respective modifiers, of scarlet macaws.

Category	Description
Hop	Jumping between nearby locations, without using any support. Wings may be open and may include up to one wing beat.
Flight	Moving between locations without using any support. Wings open and at least two wing beats.
Walk	Moving on a support by moving one foot after the other, without bill assistance.
Climb (Tripedal)	Moving upwards, downwards, or sideways on a support, using both feet and bill to assist.

Table 4. Support categories considered during observations of all behaviors, collected under locomotion protocol. NA = not applicable as no modifiers for that behavior. Modifiers apply to unstable and stable perch categories.

Category	Description	Modifier	Description
No Support	No support is being used (e.g., while flying or on the ground).	NA	NA
Unstable Perch	A structure that animals can hold on to and use to stand on, but that is not steadily attached (i.e., its position fluctuates as the animals move on it).	Thin (thickness)	Toes overlap when feet grasp the perch.
		Medium (thickness)	Feet closed around at least half the support's circumference, or fully closed around it, but loosely.
		Thick (thickness)	Feet closed around less than half the support, or with toes extended flat.
Stable Perch	A structure that animals can hold on to and use to stand on, steadily attached (i.e., its position stays unchanged as the animals move on it).	Horizontal (orientation)	Makes an angle between approximately 0° to 20° with ground (in any direction).
		Diagonal (orientation)	Makes an angle between approximately 20° and 70° with ground (in any direction).
		Vertical (orientation)	Makes an angle between approximately 70° and 90° (in any direction).
Platform	Plane structure that can be stood on but cannot be grasped with the feet.	NA	NA

Table 5. Ethogram of social-specific behaviors, respective modifiers, and social proximity categories, for scarlet macaws.

Category	Description
Allofeeding	The individual is feeding or being fed by another individual (bills connected, food transference).
Allopreening	The individual is preening or being preened by another individual (cleaning and tidying its feathers).
Nibbling	The individual gently and briefly nibbles or is nibbled by another individual, usually aimed at the bill or general head areas.
Threatening	Birds aggressively interacting, including threatening posture (head movements, feathers ruffled, mouth open) and loud vocalizations but no physical contact.
Fighting	Birds aggressively and physically interacting, including biting and feather pulling.
Chasing	An individual is chasing or being chased by another individual, with one or the other forced to move to another location.
Courtship	The individual is displaying to another individual, which may include head bobbing, ruffled feathers, vocalizations, touching bills, and back-and-forward movements on the support. Distinguished from begging behavior (from a fledgling towards parents) by the posture of the focal individual: courtship involves an elevated posture, while begging fledgling crouches on the perch.
Mating	The individual is on top or underneath another individual, cloacas are in contact, associated body movements.

Table 5. *Cont.*

Category	Description
Other interactions	Any other social interactions not included in the other categories.
Proximity scans	
Proximity (wing length)	Number of conspecifics within a wing length (~50 cm) distance of focal individual.
Proximity (2 m)	Number of conspecifics within 2 m of focal individual.

The relative location of the focal individual in each observation interval was recorded based on their position within the tree, man-made structure (e.g., buildings, electricity, post) or other natural structure (e.g., understory vegetation, clay lick, or other non-tree natural feature; Figure 2).

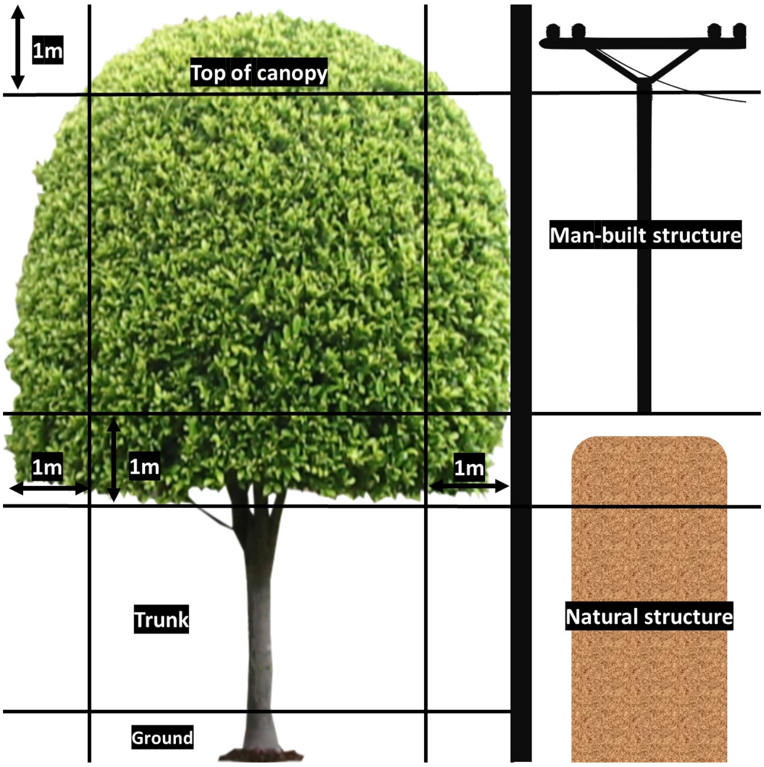


Figure 2. Diagram used for data collection on space use of free-living scarlet macaws in Costa Rica. Ground level was selected if the scarlet macaws were directly on the ground (natural such as soil or human-modified such as concrete). If close to the ground but using another structure as support, then the respective category (e.g., natural structure, such as shrubs or a clay lick wall) would be selected. Man-made structure consisted of anything not naturally occurring in the environment, such as buildings and electricity posts.

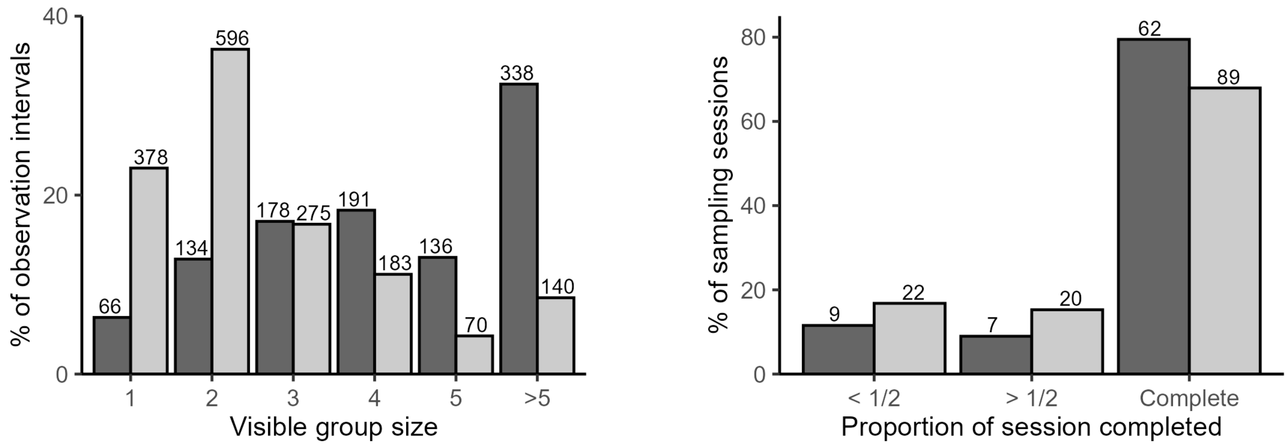
2.3. Data Analysis

Data analysis was conducted in Rstudio (R version 4.2.1; [37]), using the packages "tidyverse" version 1.3.2 [38], "lubridate" version 1.8.0 [39], "janitor" version 2.1.0 [40], and "gmodels" version 2.18.1.1 [41].

The percentages of visible group size, based on the total number of individuals observed and used for random individual selection in each observation interval, were calculated for the scarlet macaws at both locations. While the percentages of total observations (i.e., across the whole observation period) were calculated for all behaviors investigated (i.e., feeding complexity, foot use in manipulation, type of locomotion, support characteristics, type of social behaviors, and proximity to other individuals), the daily percentages of each behavior recorded were also estimated to include variations in the broad time budgets across days of observations. To compare activity across three time periods (morning: 06:00–10:59 hrs, middle of the day: 11:00–14:59 hrs, afternoon/evening: 15:00–18:00 hrs), behaviors were grouped into three activity levels (high: feeding, locomotion and object manipulation; medium: self-maintenance and social; low: perching). Although this study was mostly descriptive, a comparison of the time budgets between locations was conducted, using a Chi-squared test of independence. Adjusted standardized residuals were calculated as post hoc tests to the Chi-squared test, accounting for differences in sample size between locations, which were interpreted with Bonferroni-corrected critical values, to reduce the risk of Type I error due to the comparison of multiple categories [42]. The alpha threshold for the p-value was reduced to 0.001 to account for the non-independent data collected from the occasional repeated sampling of the same individuals.

3. Results

Data on free-living scarlet macaws were collected over 17 days, seven of those from the reintroduced population at BE and 10 from the wild population at PL, in a total of 11.4 and 12.1 h of behavioral observations, respectively. The weather was mostly clear/sunny at both locations (BE: 59%, PL: 74% of observations), it did not rain during that period, and full cloud cover was rare (BE: 5.7%, PL: 1.0%). The mean approximate temperature during observations was 28.5 °C (26–30 °C) at BE and 27.3 °C (24–30 °C) at PL. While the observations at BE were more often carried out on groups with more than five individuals, with single individuals only recorded in 6% of observations, at PL they were mostly on pairs and single individuals (Figure 3a). At BE, 79.5% of the data collection sessions were completed, while the remaining were interrupted early due to the macaws moving out of sight. At PL, the percentage of completed data collection sessions was 68% (Figure 3b).



(**a**) (**b**)

Figure 3. (**a**) Percentage of observation intervals of different group sizes of scarlet macaws included for random individual selection in group data collection, at Bosque Escondido (dark gray bars) and Punta Leona (light gray bars) in February 2022. (**b**) Percentage of 10 min data collection sessions that were complete and those that ended before ten minutes elapsed due to parrots moving out of sight. Numbers above bars correspond to total number of observation intervals across sampling sessions.

3.1. Time Budgets and Space Use

The macaws exhibited low activity (i.e., perching) more frequently in the middle of the day, while observations of medium (i.e., self-maintenance and socializing) and high (i.e., feeding, manipulation and locomotion) activities were more frequent in the morning and after 15:00 hrs, respectively (Figure 4).

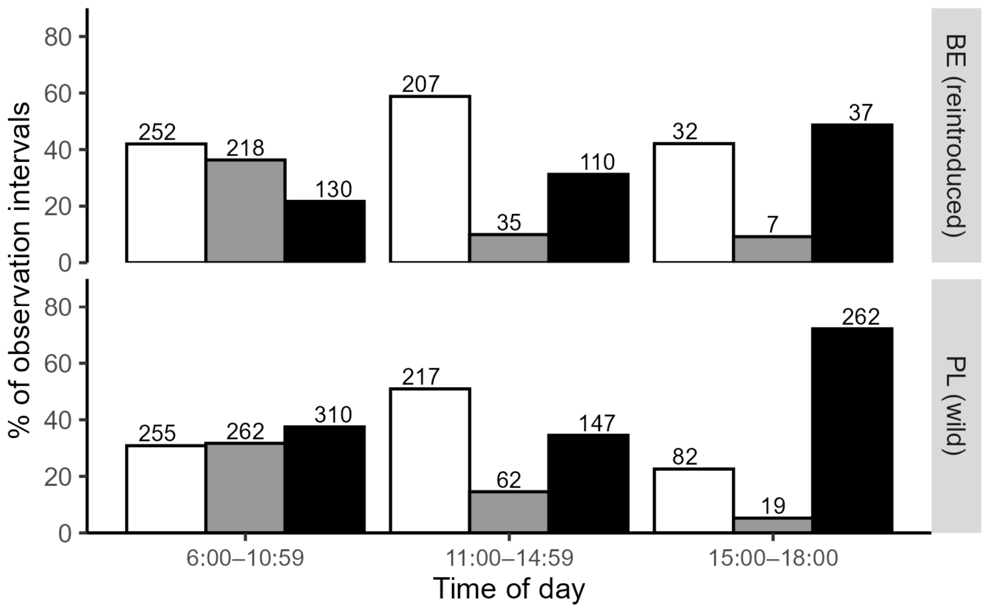
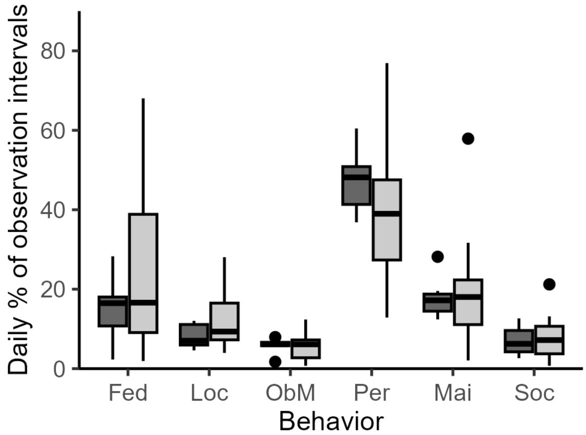
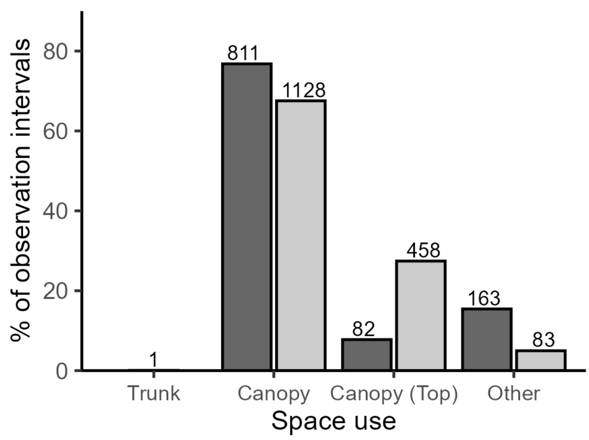


Figure 4. Total percentages of observation intervals of low- (white bars), medium- (gray bars), and high-activity (black bars) behaviors across three time periods separated by site (Bosque Escondido [BE] and Punta Leona [PL]) in February 2022. Numbers above bars correspond to total number of observation intervals across sampling sessions.

Although perching was the most common single behavior observed at both locations, it was recorded in under half the observations at both BE and PL. Therefore, most observations consisted of active behaviors (feeding, locomotion, object manipulation, self-maintenance, and socializing; Figure 5a).



(**a**)



(**b**)

Figure 5. Time budgets and space use of free-living scarlet macaws observed in Bosque Escondido (dark gray bars) and Punta Leona (light gray bars) in February 2022. (**a**) Boxplots of daily time budgets. The median, first and third quartiles are represented by the box, the whiskers represent the minimum and maximum values, and the black dots show the outliers. Fed = feeding; Loc = locomotion; ObM = object manipulation; Per = perching; Mai = self-maintenance; Soc = social. (**b**) Percentages of observation intervals of space use (i.e., tree trunk, canopy, top of canopy, other non-tree structures). Numbers above bars correspond to total number of observation intervals across sampling sessions.

While perching, the macaws were mostly inactive (BE: 61%; PL: 64% of perching observations), and comfort behaviors were rare, although there was a high proportion of perching observations where it could not be determined whether the macaws were also engaging in comfort behavior (BE: 37%; PL: 34%). Self-maintenance consisted mostly of preening (BE: 96%, PL: 93%). The activity budgets significantly differed between locations ($X^2_{(5,\ n\ =\ 2726)}$ = 112.01, $p < 0.001$; Figure 5a and Table 6). The adjusted standardized residuals (Table 6) showed that perching was more frequent in BE compared to PL, while feeding and locomotion were more frequent at PL than BE (Figure 5a).

Table 6. Summary of the Chi-squared test comparing the time budgets of the reintroduced scarlet macaws from Bosque Escondido and the wild scarlet macaws from Punta Leona, observed in Costa Rica in February 2022. Significant differences in adjusted standardized residuals, according to the corrected critical value (2.87), are shown by the blue (higher than expected counts of that behavior in that location) and red cells (lower than expected counts of that behavior in that location).

X^2	df	*p*-Value	Adjusted Standardized Cell Residuals		
			Corrected critical value: 2.87		
				Bosque Escondido (reintroduced)	Punta Leona (wild)
112.01	5	<0.001	Feed/drink	−8.47	8.47
			Locomotion	−4.27	4.27
			Object manipulation	2.63	−2.63
			Perching	6.91	−6.91
			Self-maintenance	2.19	−2.19
			Social	0.86	−0.86

The tree canopy was the preferred location of the scarlet macaws at both locations (Figure 5b). Use of the tree trunk was rare in both locations (Figure 5b), and other (non-tree) structures were also rarely used and consisted mostly of artificial feeders (BE) and nest boxes (PL). The macaws in both locations were mostly observed at heights over 10 m, were never seen on the ground, and were rarely close to it. Similarly, the trees and other structures they used to perch on were predominantly of heights over 10 m.

3.2. Feeding and Object Manipulation Behaviors

Over 90% of the feeding observations at BE (*n* = 133) were on the artificial feeders rather than naturally occurring food. The food trays high in the trees obscured visibility and it was not possible to determine what the scarlet macaws were eating in 82% of the observations. At PL, this was not an issue (because there were no artificial feeders) and only 5% of feeding observations were unclear. Out of the feeding observations that were recorded at BE that allowed for the type of manipulation used during feeding to be determined (*n* = 24), 71% were of intermediate manipulation complexity, 12.5% were passive manipulation, with basic and advanced complexity accounting for only 8% (each) of the observations. In contrast, clearly visible feeding observations at PL (*n* = 207) consisted mostly of advanced manipulation (65%), followed by intermediate manipulation (34%). Basic food manipulation was not observed at PL, and passive manipulation only accounted for 1% of feeding observations (Figure 6a).

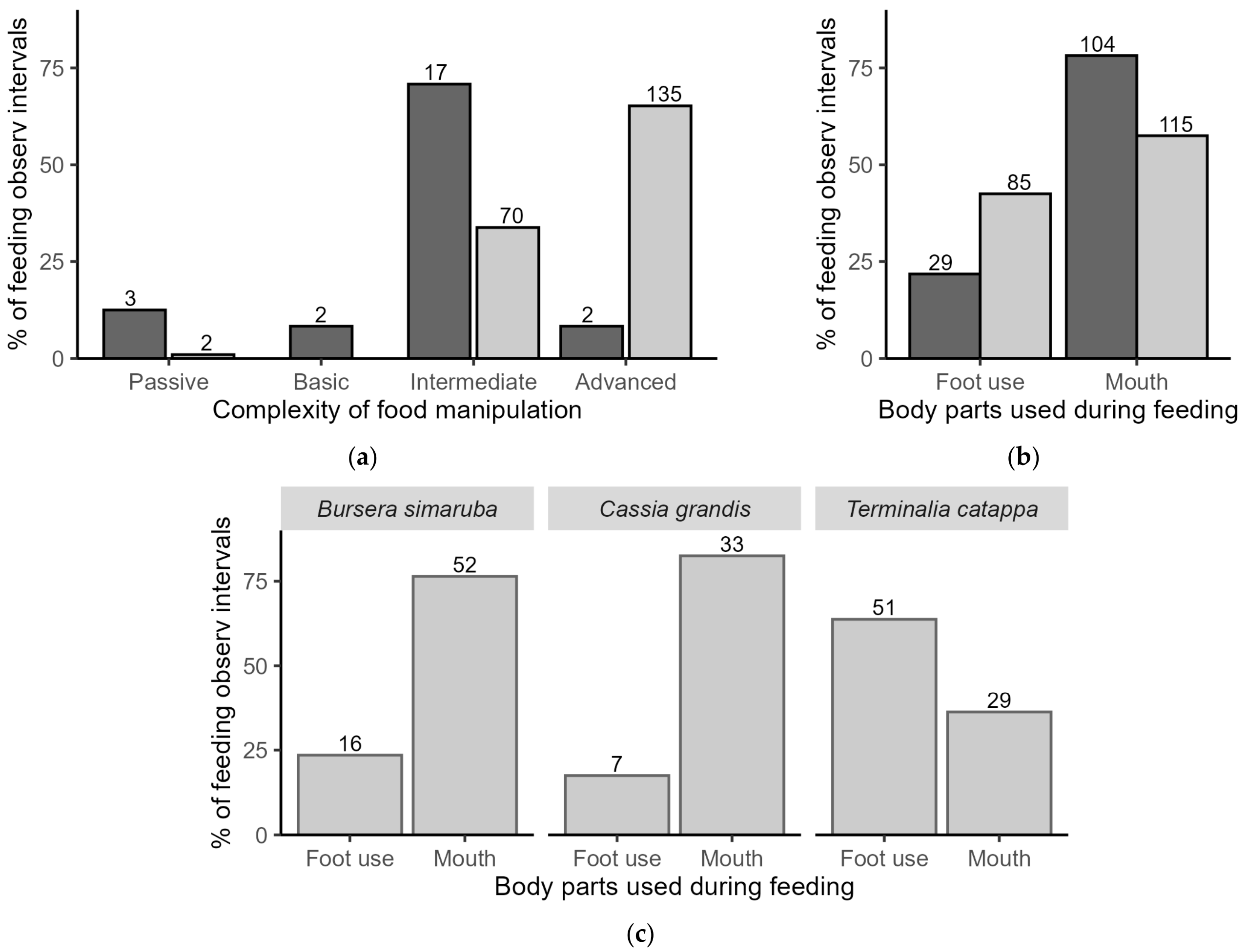


Figure 6. Food manipulation and foot use in free-living scarlet macaws observed in Costa Rica in February 2022. Percentage of feeding observation intervals from the scarlet macaws at Bosque Escondido (dark gray bars) and Punta Leona (light gray bars) for (**a**) different levels of food manipulation (**b**) body parts used for feeding/food manipulation, (**c**) body parts used for feeding/food manipulation on the fruits from gumbo limbo (*Bursera simaruba*), pink shower tree (*Cassia grandis*), and Indian beach almond tree (*Terminalia catappa*) at PL. Numbers above bars correspond to total number of observation intervals across sampling sessions.

The scarlet macaws at BE used their feet for food manipulation in 22% of feeding observations (n = 133; Figure 6b). The visual obstacles reported above for feeding observations at BE did not interfere with the recording of the body parts used for food manipulation, as it was still possible to see whether they were using their feet while feeding in most observations. At PL, general foot use in feeding was relatively high (42.5% of feeding observations; n = 200; Figure 6b), but it differed across the three plant species they were seen feeding on (Figure 6c).

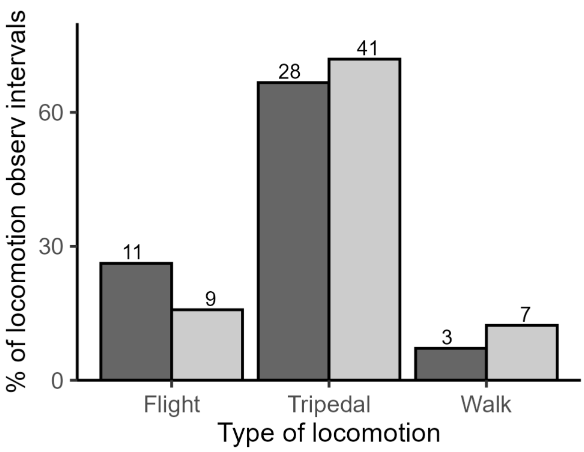
The gumbo-limbo (*Bursera simaruba*; 38% of feeding observations) produces a small spherical fruit (~1.5 cm diameter; Figure 7a) on which the scarlet macaws were seen feeding. These fruits were often located at the extremities of branches, so the macaws had to navigate the nearby branches and explore several positions to reach them. Once they reached the fruit, they either consumed them directly without the aid of their feet (76% of observations) or they used their feet to adjust the fruit's position or aid in its manipulation. In the case of the pink shower tree (*Cassia grandis*; 22% of feeding observations), the fruits are up to 50 cm long (Figure 7c), and to feed on them, the scarlet macaws were seen hanging from nearby vertical perches or the fruit itself to extract the seeds within. They used their feet in 17.5% of the feeding observations on this species (Figure 6c) to pull the fruit towards their bills and/or to keep it in position while eating. Indian beach almonds (*Terminalia catappa*; Figure 7b) accounted for 40% of the feeding observations, and the scarlet macaws were observed pulling the fruit off the tree with their bills and, in 64% of the observations on this species, holding it in their feet while manipulating and consuming it (Figure 6c).

(**a**) (**b**) (**c**)

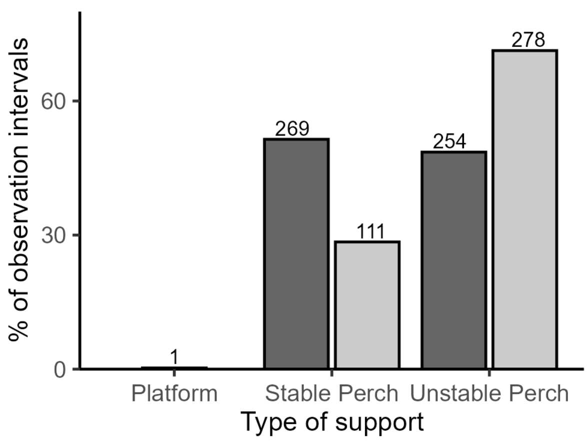
Figure 7. Food items in the diet of wild scarlet macaws observed at Punta Leona (Costa Rica) in February 2022. Dropped fruits of (**a**) gumbo-limbo, *Bursera simaruba*; (**b**) beach almond, *Terminalia catappa*, after manipulation from a scarlet macaw; (**c**) pink shower tree, *Cassia grandis*, after manipulation and seed extraction from a scarlet macaw. Photos: Ricardo Lemos de Figueiredo.

3.3. Locomotion and Support Use

Tripedal locomotion (i.e., climbing with the aid of the bill) was the predominant type of locomotion of the scarlet macaws at both locations (Figure 8a). Flying was infrequently recorded in the observation intervals (Figure 8a), and although macaws were seen flying in both locations, sometimes covering distances at least as long as the degree of vision allowed, these observations were not recorded. BE's scarlet macaws used stable and unstable perches evenly, while scarlet macaws at PL were mostly seen on unstable perches (Figure 8b). The thickness of supports used was relatively homogeneous in the scarlet macaws at BE, while the birds at PL used thin perches in most observations (Figure 8b). Support orientation was similar at both locations, with horizontal perches used in approximately half of the observations, while the use of diagonal perches was also relatively high at both locations (Figure 8c). The birds exhibited an apparent high confidence (i.e., with little visible hesitation) in climbing the diversity of supports in their environment and at PL, especially, they seemed to navigate the tree branches, including the more challenging thin, unstable, and/or non-horizontal ones, with relative ease.



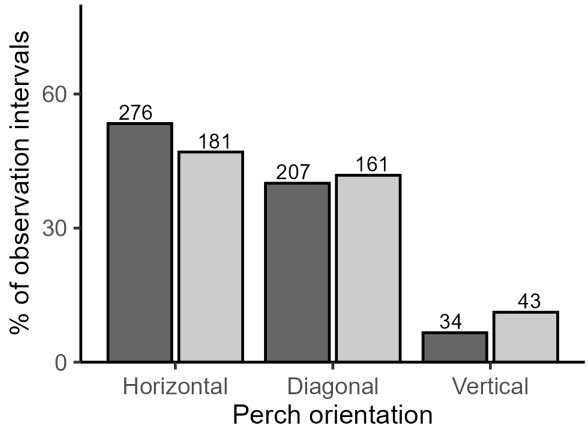
(**a**)



(**b**)

Figure 8. *Cont.*

(**c**)

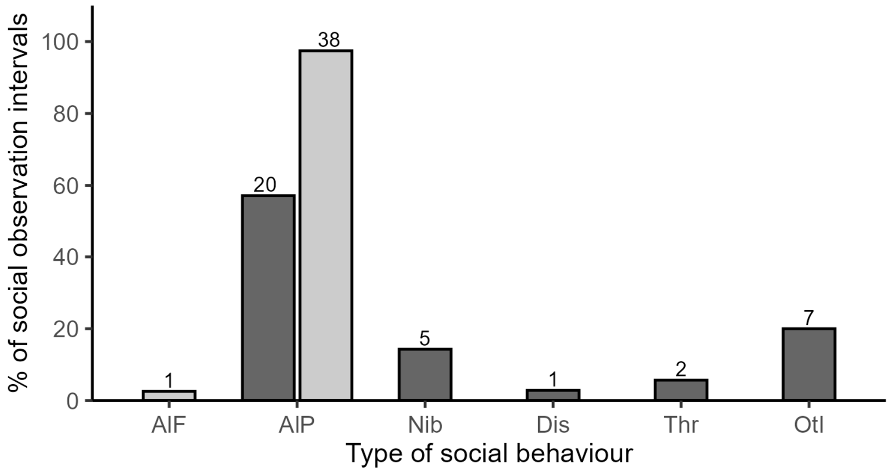


(**d**)

Figure 8. Locomotion and support use in the scarlet macaws at Bosque Escondido (dark gray bars) and Punta Leona (light gray bars) in February 2022. (**a**) Percentage of observation intervals for each type of locomotion; (**b**) percentage of observation intervals for each type of support used; (**c**) percentage of observation intervals for support use in each thickness category; (**d**) percentage of observation intervals for support use in each orientation category. Numbers above bars correspond to total number of observation intervals across sampling sessions.

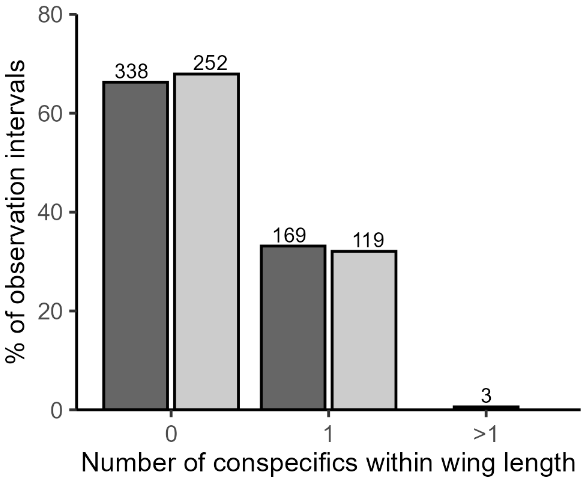
3.4. Social Behavior and Proximity

The social behavior observed at PL was almost entirely allopreening, but a higher diversity of social behaviors was recorded in BE's scarlet macaws, even though allopreening was still the most common one (Figure 9a). Only in 33% (BE, n = 169) and 32% (PL, n = 119) of observations did the scarlet macaws have a conspecific within a wing length. With BE's scarlet macaws, there were three instances (<1%) of more than one individual within wing length (Figure 9b), which was not observed at PL. The majority of observations showed at least one conspecific within 2 m of the focal bird, in both locations (Figure 9c).

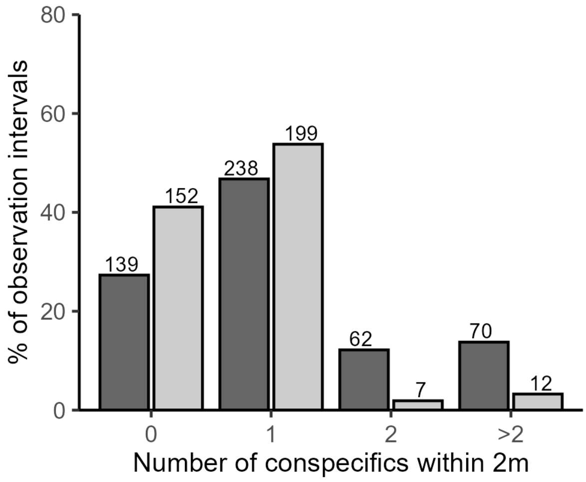


(**a**)

Figure 9. *Cont.*



(**b**)



(**c**)

Figure 9. Social behavior and proximity to conspecifics of free-living scarlet macaws observed in Costa Rica in February 2022. Percentage of (**a**) each type of social interaction, (**b**) number of individuals within wing length of focal bird, and (**c**) number of individuals within 2 m of focal bird, observed on the reintroduced scarlet macaws at Bosque Escondido (dark gray bars) and the wild scarlet macaws at Punta Leona (light gray bars). Numbers above bars represent total number of observation intervals across sampling sessions. Types of social behavior: AlF = allofeeding; AlP = allopreening; Nib = nibbling; Dis = displacement; Thr = threatening; and OtI = other interactions.

4. Discussion

Our observations suggest that the scarlet macaws at both locations were active in most observations. The scarlet macaws also exhibited a preference for height when on a support, engagement in complex food manipulation (at PL), and use of high diversity of supports, while differences in group sizes were also detected between locations.

4.1. Inactivity, Self-Maintenance, and Activity Patterns

The scarlet macaws at both locations displayed active behaviors in most observations, although perching was the most common single behavior observed. Perching consisted of resting or alert behavior, both important behaviors for survival in the natural environment. While resting allows birds to reduce energy expenditure [43] and avoid overheating [44], alert behavior or vigilance is beneficial for predator detection and avoidance [45]. The significantly higher proportion of perching observations at BE could be a reflection of the facilitated access the scarlet macaws there had to food because of supplementary feeding, and/or due to them having been reared, and released from, captivity. Furthermore, self-maintenance, and mostly preening, was also frequently seen, which is expected, as it is an advantageous behavior that allows birds to clean their feathers and skin, and remove parasites [46]. It has been suggested that preening can be a comfort behavior [47], and a response to stress (i.e., post-predator detection) in wild birds [48]. There was no visible predator detection in the present study, and therefore, its effects on preening behavior cannot be confirmed. It is possible human disturbance influenced this behavior, but there were no significant differences in self-maintenance between locations, despite the scarlet macaws at PL being more exposed to humans.

A bimodal pattern of activity has been reported across parrot species in the wild, with peaks of activity in early morning and late afternoon, and mostly resting and other low-activity behaviors in the middle of the day [49–51]. Observations of low activity (i.e., perching) showed a similar pattern, with the highest proportion in the middle of the day. The increased proportion of high activity later in the day, especially at PL, also agrees with the activity patterns previously reported for free-living parrots [49–51], although there were few differences between morning and middle of the day at both locations. As long-range movements were not recorded, it is possible that the scarlet macaws reduced flight activity in the middle of the day, but still remained active within the same area (e.g., activities within the same tree), which has been observed in grayheaded parrots (*Poicephalus fuscicollis*), on days with cooler temperatures [52]. Self-maintenance and socializing (i.e., medium activity) were most frequent in the morning, and although these behaviors have been observed throughout the day in previous studies, they have also been observed before and between feeding bouts [51,52].

The scarlet macaws were within the tree canopy in most observations, which concurs with the known arboreal habit of macaws [53,54], which may offer advantages such as lower risk of predation and disease [55]. A preference for heights, also consistent with their arboreal habit, was clearly observed, as they most often stayed high in the trees, and at PL, they were also often seen on the top of the canopy. They also avoided the ground and only on rare occasions were they below 10 m from the ground. This preference for heights has been suggested in previous studies focusing on their diet, as they feed mostly from trees, on the canopy [33,56], and have also been observed drinking water from hollows on the tree trunks [56], potentially reducing the need to descend to the ground to drink.

4.2. Feeding and Object Manipulation Behaviors

The scarlet macaws at PL were feeding in over a quarter of observations, engaged mostly in complex manipulation, and used their feet in almost half the feeding observations. However, they were seen feeding on only three tree species, a small sample of the species that have been previously reported to be part of the diet of scarlet macaws in Costa Rica [33]. No other potential food sources for the macaws were observed in the locations used for observations, which was also confirmed by the local ecologists working with the species in the area (R. Taylor, pers comm., 2023). This could have been due to a combination of seasonal variations in food availability [33] and the present study's restriction to a small part of the season and limited number and diversity of locations to conduct behavioral observations. Nevertheless, the scarlet macaws showed a diversity of foraging behaviors within and across those three plant species. They had to adapt their locomotion, position on the branches, and/or use their mouth and feet to reach and manipulate the different sized and shaped fruits and seeds. This behavioral flexibility influenced by the diversity of food sources in the environment has been previously highlighted across macaw species. For example, a pair of adult scarlet macaws, also in Costa Rica, was observed removing hanging palm nuts (*Scheelea rostrata*) mid-air and taking them to nearby perches for consumption, while their offspring, two juveniles, were feeding from a nearby tree, presumably not yet able to feed from the more difficult-to-reach palm nuts [16]. Blue-and-yellow macaws (*A. ararauna*) were also seen feeding on unripe slash pinecones (*Pinus elliottii*) in an urban area in Brazil, an exotic species that they adapted to feed from in a human-dominated environment [24], while green-winged macaws in Venezuela had to use their feet and bills to open the hard nuts of multiple tree species [57].

The scarlet macaws at BE were mostly seen feeding from the artificial feeders, and although some of the food items provided required more complex manipulation (e.g., corn cob), the tray set-up likely facilitated direct consumption, with less need for foraging-related behaviors such as searching for food and manipulation. This facilitated access to food could explain why the percentage of feeding observations was significantly lower for the scarlet macaws at BE than PL, as it has been previously suggested that parrots adapt their foraging strategies according to resource availability [58]. Supplementary feeding is an important factor in the success of parrot reintroduction programs [59], and released parrots have been found to gradually rely less on it as they start dispersing and consuming wild foods [60,61]. In the present study, no conclusions can be made on the dispersal rates or wild-type foraging skills of the released scarlet macaws at BE, as they were not individually tracked. Furthermore, despite confirmation of local staff that released macaws were seen feeding on wild foods (M. Gonzaléz, pers comm., 2022), this was very rarely observed in the present study, likely because observations were limited to the release site and surrounding areas, and therefore, biased towards the individuals that were still reliant on the artificial feeders.

4.3. Locomotion and Support Use

The significantly lower percentage of locomotion detected in the scarlet macaws at BE could have also been related to their easier access to food resources (i.e., reduced need to move within the trees searching for food), or captivity-elicited deficiencies in locomotion skills in comparison to their wild-born counterparts, as previously reported for other species (e.g., golden-lion tamarins *Leontopithecus rosalia*; [62]). The scarlet macaws at both locations mostly climbed while moving around the tree canopy. Parrots are proficient climbers, using several body parts (e.g., bill, feet, tail) to achieve balance and push and pull themselves across branches and other supports [63]. Their climbing proficiency was also noted in the variety of supports they used, with the scarlet macaws at both locations using unstable, thin, and non-horizontal perches in relatively high proportions, even though they are more challenging to hold onto. No quantification of support characteristics used by free-living parrots has been found in the literature, and therefore, this may be the first. However, as scarlet macaws in the wild forage on several parts of multiple tree species [32,55], it can be assumed they have to frequently navigate a challenging variety of tree structures to reach their food. Furthermore, their climbing abilities, and the challenging supports they use, are also highlighted by how they can hold on to and climb up vertical clay licks for geophagy (i.e., voluntary soil ingestion) [64], which offer few opportunities for support grasping [63].

The heterogeneity and complexity of supports they have to navigate may also explain the low proportions of walking that were observed. Even when moving horizontally, parrots often use their bills (and therefore tripedal locomotion/climbing) together with their feet for balance [63], if the supports they are on are not stable under their weight. The low proportion of flights in the time budget, however, is most likely an underestimation resulting from the sampling method, as (1) only visible individuals in each observation interval were sampled, and flying individuals often moved out of sight, and (2) short flights within trees or between neighboring trees were often quick events and not captured by the interval sampling point. Furthermore, although flights were noticed in qualitative observations, further research is required to understand how often, and for how long, free-living scarlet macaws spend flying.

4.4. Group Size, Social Behavior, and Proximity

The reintroduced population at BE had bigger observable group sizes for random individual selection than in PL, and more often showed higher numbers of individuals within 2 m of the focal bird in the proximity scans. These results were likely influenced by several factors. First, most of the observations at BE were at or relatively close to the supplementary feeding site, where the released macaws gathered for feeding, and therefore, bigger groups were to be expected. Furthermore, as the macaws at BE were captive-bred, and no older than seven years old, they likely moved shorter distances from the point of release than their wild-hatched counterparts at PL, and stayed around the release area with their peers. Post-monitoring data from two other parrot reintroduction programs showed that the captive-bred individuals, and especially the younger ones, generally stayed within the release area [61]. Furthermore, unlike the released parrots in both these studies, who had the opportunity to flock with wild-hatched conspecifics and likely benefited from social learning of wild-type behaviors and skills [61], the scarlet macaws at BE were reintroduced into an area without a local wild population. As social learning plays a key role in the behavioral development of scarlet macaws [19], the released individuals at BE may therefore take longer to develop the necessary skills before ranging greater distances.

The scarlet macaws at PL were more often observed in pairs, although there were also observations of single individuals and small groups. These data agree with previous studies on wild scarlet macaws, suggesting that they sometimes flock in large numbers [65], but more often travel in pairs or small family units [48]. Social behavior was observed in a relatively low proportion of observation intervals, and wing length proximity had similar proportions in both locations. Although allopreening was the more common social behavior in both populations, at BE, several other interactions were also observed. As mentioned before, the population at BE was young, and likely engaged in social play, as previously reported in this species [19]. No breeding had yet been confirmed among the scarlet macaws at BE, but the records of allopreening, which serves both hygienic and social purposes [66], plus qualitative observations, suggest that pair bonding has occurred within that population. At PL, pair bonding was shown by allopreening and further confirmed by on-going breeding during this study's period of observations, as the team of researchers that monitors the local scarlet macaw population reported the presence of chicks of various ages in both natural and artificial nest boxes (R. Taylor, pers comm., 2022).

4.5. Applications of This Study to Ex Situ Management

The outcomes of this study can inform ex situ management of scarlet macaws in several ways. The behavioral data collected from free-living macaws can be used for direct comparisons with captive macaws, facilitating the detection of abnormal behaviors and/or missing wild-type behaviors in the latter, which can be an indicator that their behavioral repertoire is being inhibited and/or modified by the ex situ environment. Furthermore, this study's assessment of how free-living macaws utilize and interact with their environment can inform enclosure design and husbandry. For example, the preference for height demonstrated by the free-living macaws in this study, and their use of varied and complex supports during perching and locomotion, may indicate that in captivity they would benefit from a complex support/perch system and opportunities to perch high within the enclosure. Similarly, the variety of behaviors demonstrated by the wild macaws to reach and manipulate food items suggests that presentation of food to captive macaws should be varied and complex. Thus, ex situ behavioral assessments and management modifications informed by in situ data can facilitate welfare improvements and improve the success of ex situ conservation programs.

4.6. Limitations of the Study

As a result of time constraints, the behavioral observations were conducted in a short period of time and in a low number of locations, which did not reflect the species' wide geographic distribution across Central and South America. Therefore, this study does not account for potential differences in behavior across seasons (e.g., breeding vs. non-breeding season; seasonality in food availability) and populations. Within both locations, only certain areas could be accessed for data collection, which likely biased observations towards certain individuals and behaviors. Furthermore, the macaws at both locations were exposed to high levels of human disturbance, which could have affected their behavior, although it also means the presence of the observer likely did not affect the birds. The locations of this study also differed in type of habitat, which potentially confounded differences in behavior between the wild-hatched macaws at PL and the captive-hatched macaws at BE.

Therefore, further studies should assess the behavior of free-living scarlet macaws throughout their geographic distribution and across seasons. More behavioral data from both wild-hatched and captive-bred birds across habitats would also help in understanding how reintroduced macaws adapt to their new environment over time.

5. Conclusions

Despite the limitations of this study, it provides new insights into the behavioral ecology of free-living scarlet macaws, including, to our knowledge, the first quantitative descriptions of foot use in manipulation and support characteristics. The overall findings suggest that the free-living scarlet macaws in this study (1) were generally active, varying their activity levels throughout the day; (2) preferred to stay high in the tree canopy and avoided descending to the ground or close to it; (3) showed complex feeding behaviors, adapting to varied food items with different foraging strategies, including foot use;

(4) navigated and perched on a high diversity of supports, and used challenging (i.e., unstable, thin, and non-horizontal) structures at least as often; and (5) were more often seen alone, in pairs or small groups, in the natural population at PL, and bigger groups in the reintroduced population at BE. This study was planned and conducted with the primary goal of generating evidence to inform ex situ management and husbandry. Data from free-living parrots can be used for behavioral comparisons with captive counterparts to better understand which behaviors naturally occur in the species and which behaviors are a result of the captive environment. Furthermore, by understanding how free-living macaws interact with their environment, which features of the natural habitat that need to be replicated in ex situ enclosures to enable wild-type behaviors can be determined, with the potential to improve animal welfare and ex situ conservation programs.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/jzbg5040044/s1, Detailed description of methodology used for random individual selection during group sampling. Figure S1: Schematic representation of the method for random selection of individuals during focal interval sampling of groups, used while sampling free-living scarlet macaws in Costa Rica.

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Institutional Review Board Statement: The animal study protocol was approved by the Ethics Committee of the University of Birmingham (ERN_19-0974, approved on 1 October 2018).

Data Availability Statement: Data are contained within the article.

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Conflicts of Interest: The authors declare no conflicts of interest.

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