The value of behavioral activity records for conservation breeding: the case of Spix's macaw in human care

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Abstract: The Spix's macaw (*Cyanopsitta spixii*), extinct in the wild since 2019, is currently maintained in *ex situ* breeding facilities. Captive breeding expanded the global population from 53 individuals in 2000 to ca. 400 by December 2025, enabling two soft releases. To support reintroduction, we developed an ethogram of 85 behaviors and 1357 quantitative records based on the observation of 123 birds in the facility ACTP Germany, recorded the time activity patterns of ten pairs, and analyzed their breeding output. We tested whether behavioral compatibility—measured here as time-activity synchrony—should complement genetic criteria to improve breeding output. Individual activity patterns were consistent, but females were markedly more synchronized with their mates than with other males. However, a synchrony threshold of at least 75% seemed necessary for successful breeding. Adjusting pair matching based on synchrony and improving general husbandry conditions (diet & enrichment) led to higher breeding output: pairs raising chicks increased from 0 in 2019 to 16 in 2024, fertility rates increased from 39% in 2019 to 60% in 2024, and annual chick output increased from 11 to 44 between 2019 and 2024. These results, based on 86 forced mating attempts, champion the idea that systematic behavioral monitoring can substantially enhance conservation breeding in monogamous parrot species.

Keywords: *Cyanopsitta spixii*, ethogram, extinct in the wild, pair formation, stereotypies, synchrony, time activity patterns

1. Introduction

The Spix's macaw (*Cyanopsitta spixii*) is a monotypic psittacine of the Arini clade, currently classified as extinct in the wild (Butchart et al. 2018, Birdlife International 2024). After Johann Baptist von Spix first observed it about 200 years ago, the species was formally described by Wagler in 1832 (Barros *et al*. 2012). Historical sightings or reports remained rare for the past two centuries (Barros *et al*. 2012). In the 1980s, a tiny population of five individuals was rediscovered near Barra Grande and adjacent Riacho Melância in north Bahia (Roth 1990a, 1990b). Between 1987 and 1988, the remaining three individuals from the only known population found their way into the illegal wildlife trade (Collar 1992). A single male was discovered in the wild near Riacho Melância in July 1990, but no females were present. In 1995, one female held in captivity was released into the wild, the individual died shortly after and thus this reintroduction attempt failed (Juniper 2002). The last free-ranging male was not seen after October 2000, leading to the classification of the species as "extinct in the wild" in 2019 (Butchart et al. 2018, Birdlife International 2024) and the initiation of a global *ex situ* breeding program (Juniper 2002). From an initial captive population of 53 individuals by December 2000 (Purchase 2019), the population in human care grew to ca. 400 individuals as of December 2025. Despite this apparent success, little is known about how the reproductive output could be improved for future conservation efforts since little is known about the behavior, ecology and breeding biology of the species.

Behavioral data are essential for establishing adequate husbandry guidelines (Luescher 2006) and improving conservation breeding for reintroduction programs (Plair et al. 2008, de Azevedo et al. 2017). This includes the elimination of stereotypies in birds in human care, as this is not only an issue of animal welfare but also likely to affect the competence of individuals released into the wild. Much behavioral research has been dedicated to psittacines over the past decades, ranging from descriptions of behaviors (Dilger 1960, Hardy 1963, Buckley 1968, Serpell 1979, Levinson 1980, Uribe 1982, Lantermann 1987, Rowley 1990, Prestes 1991, Schneider *et al*. 2006, Favoretto *et al*. 2024) to studies testing specific behavioral hypotheses or assessing complex behavior paradigms in cognitive behavior, communication or the effects of environmental enrichment (Pepperberg 2000, Dahlin & Wright 2007, Auersperg & von Bayern 2019, Checon *et al*. 2020, Ramos *et al*. 2020).

In macaws, detailed behavioral descriptions are only available for free-ranging populations for the Blue-winged macaw (*Primolius maracana*; Barros 2001, in the wild) and the Red-fronted macaw (*Ara rubrogenys,* Christiansen & Pitter 1992, Pitter & Christiansen 1995, 1997), and for populations in human care for the Scarlet macaw (*A. macao*, Uribe 1982), Blue-and-gold macaw (*A. ararauna*; Uribe 1982), and Lear's and Hyacinth macaw (*Anodorhynchus leari* and *A. hyacinthinus*, Schneider *et al*. 2006, Favoretto *et al*. 2024). Hence, the behaviors of many New World parrots remain little investigated, reducing the scope for improvements in conservation breeding. The first aim of this study was therefore to provide a complete overview of behaviors in Spix's macaw, including stereotypies and other behavioral disorders.

A critical aspect of the behavior of birds in human care is the time-activity pattern. Time-activity patterns differ substantially between conspecific individuals from in-situ and *ex situ* populations (Cornejo *et al.* 2005). Easy access to food and obvious differences in the structure of the local environment often induce shifts in time-activity patterns for parrots in human care. Previous studies indicate that such birds spend predominantly their time resting or performing maintenance behaviors (Lantermann 1998, Cornejo *et al.* 2005, de Azevedo *et al*. 2016, Checon *et al*. 2020, Ramos *et al.* 2020). The increase in time spent resting at the expense of foraging activity and a captive environment with a reduced structure are serious concerns as they may be linked to the emergence of behavioral disorders such as stereotypies (Meehan et al. 2004, Garner et al. 2006). The second goal of this study was therefore to establish a baseline of the time-activity patterns in Spix's macaw under standard husbandry conditions. This will allow an assessment of alternative enrichment protocols and help identify those which ensure that time-activity patterns of individuals in human care approach those of wild parrots.

Psittacine *ex situ* programs often emphasize the importance of matching individuals in ways that minimize inbreeding (Morrison *et al.* 2020). However, pairings based on sole genetic criteria may not necessarily be successful, as such pairing designs can trigger aggression and/or be associated with low breeding success in several psittacine species (Waugh & Romero 2000, Luescher 2006). Spix's macaw is no exception, and once artificial insemination was discontinued in 2018, genetically-informed pairings often resulted in infertile clutches or in individuals not showing any interest in breeding (see Results). Among the community of people breeding parrots, there is a consensus that behavioral compatibility is crucial for breeding success and that a high level of behavioral synchrony among partners is desirable. Unfortunately, there is very limited information available on how behavior relates to breeding success. If such a link existed, time-activity patterns might have the potential to guide *ex situ* breeding efforts and complement genetic choice criteria already in use. Our third and final goal was therefore to assess the relevance of synchrony in time-activity patterns between paired males and females by examining the relationship between synchrony and breeding output.

2. Materials and Methods

2.1 Husbandry

To achieve our three objectives, we recorded the behavior of 123 Spix's macaws, on a weekly basis, in the largest *ex situ* population in the world during 2018 and 2019. We also studied diurnal time activity patterns and behavioral synchrony of ten breeding pairs outside the breeding season (September-February) during those two years. The study took place in the facility of the Association for the Conservation of Threatened Parrots e. V. (ACTP) in Rüdersdorf, Brandenburg, Germany, where all Spix's macaws are housed as pairs if adult or in flocks if the birds were still immature in partly isolated units. Each unit consists of 12 or 13 aviaries, which were subdivided into smaller subunits of 4–5 aviaries, each separated by a single indoor corridor. The subunits are insulated for noise so that only the pairs located within the same subunit maintained auditory contact with each other while inside. Each aviary had an indoor and outdoor enclosure, with dimensions of 2 × 3.5 × 2.8 m and 16 × 2 × 3 m (length x width x height), respectively. The indoor aviary was heated to 18–21 °C from October to March and includes a restricted selection of horizontal and diagonal perches (to encourage the use of the maximum flight area), two feeding tables accessible from the corridor, an L-nest box and various elements for environmental enrichment. The tiled floor in each inside enclosure was covered with a 2–3 cm thick layer of wood shavings. Each box was equipped with two high-definition cameras (Vicon V988D-W311MIR Dome Camera): one inside the unit and one inside the nest. These cameras record the activities of the birds for a period of several consecutive weeks, with video files stored externally on a computer server. Outdoor enclosures consisted of individual constellations of perches and a canopy (1 m), which protected the birds from direct sun exposure or excessive rain. An artificial rain system was installed in all outdoor aviaries, which was operated on an automated schedule over the warmer months (April-September).

All birds were fed twice daily (08:00–09:00 and 15:30–16:30 pm) and supplied with additional pellets during the breeding season lasting from March–August. Food quantity was adjusted in the winter and a maintenance diet for adults was implemented to counteract excessive weight gain and ensure the maintenance of birds close to desired body weights (female: 288 g, male: 318 g, average weights of n = 112 birds) during both semi-annual periods (breeding and nonbreeding). Water was provided *ad libitum*. At the beginning of the breeding season in March, the amount of food was increased, and vitamins and minerals were added. Further changes were implemented once pairs began to rear chicks.

2.2 Observation methods

Non-contact observations were carried out using video cameras to avoid behavioral changes influenced by the presence of an observer. In total, 320 hours of video material were analyzed in 60-minutes slices for the establishment of the behavioral repertoire and the quantification of time-activity patterns. The video sequences were stored externally (AVI format) and analyzed with Avidemux (v. 2.7.4). Behaviors for the ethogram were categorized in ten distinct categories (Fig. 1), which are described in detail in the Supplementary Information, including *maintenance behaviors* (all behaviors included in SI 2a, behavior 1 to 12), *physiological behaviors* (see SI 2b, behavior 1 to 5), *locomotion behaviors* (active forms; SI 2c, behavior 1 to 3), *inactivity behaviors* (SI 2d, behavior 1 to 3), *agonistic behaviors* (SI 2e, behavior 1 to 13), *displacement behaviors* (SI 2f: behavior 1 to 11), *submission behaviors* (SI 2g: behavior 1 to 11), *social behaviors* (SI 2h: behavior 1 to 7), *sexual behaviors* (SI 2i: behavior 1 to 8) and *behavioral disorders* (SI 2j: behavior 1 to 12). This classification expands a preliminary survey which focused on agonistic and submission behaviors (Marcuk et al. 2020). The behaviors of each individual were analyzed during the full diurnal period (from 05:00 to 21:00, light hours).

Time-activity patterns were recorded for ten pairs, where the duration of each behavior was analyzed for each hour rounded to the nearest second and assigned to the respective behavior category. Displacement behaviors were lumped together with submission or agonistic behavior because of their very short duration. Since time activity patterns were observed exclusively in indoor enclosures, neither heat display nor ruffling was observed. Therefore, physiological behaviors mostly accounted for active "foraging time" (e.g., food and water intake, defecation). Time activity patterns were also recorded during the non-breeding season. Therefore, behaviors related to sexual activity (social behaviors 4 to 7, sexual behaviors 1 to 8, and behavioral disorders 11 to 12) were excluded from the analysis of time activity patterns.

We selected these pairs so as to capture a wide range of demographic history, with the constraint that we could only retain pairs for which the male and the female were morphologically sufficiently different to unambiguously assign records to individuals based on plumage aberrations, bare parts resulting from plucking, different iris coloration or, on some occasions, the color and variation of the leg bands. All 20 individuals were hand-reared.

The interior was standardized for all indoor enclosures to minimize the impact of environmental factors on the behavioral repertoire or activity period of the birds during the observation period. None of the nest boxes were open, ensuring that none of the pairs included in this study express sexual behaviors. The observations were conducted during the early non-breeding season at the beginning of September in 2018 (three pairs; 5–8 September) and 2019 (seven pairs; 2–4 September). All individuals were adults (minimum age was 4 yrs). The observations took place before an enrichment plan was initiated in mid-September 2019. The recorded time activity patterns thus constitute a baseline treatment without the influence of any sort of environmental enrichment. Breeding data were collected for the ten pairs between 2014 and 2024 at Al Wabra Wildlife Preservation and ACTP Germany. We recorded for each female the number of eggs being laid, the number of fertile eggs, and the number of weaned chicks produced. Eggs and chicks resulting from artificial inseminations were not included. All eggs were inspected with a light source (i.e., candled) at least once to determine whether an embryo was developing or not. We also counted the total number of offspring once they were weaned.

2.3 Data analysis and statistics

To assess behavioral synchrony, we excluded social behaviors, since interactions must necessarily occur in synchrony. We also excluded behavioral disorders since mates were never observed to mirror such behaviors. As mentioned above, both the timing of the experiment and its design precluded the expression of sexual behaviors. Using this data, we first performed a hierarchical cluster analysis (type = Ward, average type = Euclidean, k = 10 clusters, equal to the number of pairs) to determine whether the actual pairs were identified as clusters on the basis of their time-activity patterns. The clustering and its representation were compiled using OriginLab 2025 (OriginLab Corporation, Northampton, MA 01060 US). Second, we computed a synchrony index for each single pair to quantify the observed similarity in time activity patterns. The synchrony index *S* was defined as the sum of absolute differences between the percentages *p* which each behavior was displayed in each hour ($\text{hour}_1 \ldots \text{hour}_{17}$) of the male (♂) and the female (♀), as:

$$S = \sum_h \sum_b \left| \frac{p_{hb\,♂} - p_{hb\,♀}}{H \times 100} \right| \quad (1)$$

where *h* is the index of each hourly period between 05:00:00 and 21:59:59 (i.e., 05:00:00–05:59:59, 06:00:00–06:59:59, ..., 21:00:00–21:59:59), *b* is the index of each behavior category considered (i.e., maintenance, foraging, submission, agonistic, resting & locomotion), and *H* is the total number of hourly periods recorded (here 17). A synchrony index of 0 represents the lowest conceivable similarity of the time-activity behavior patterns between female and male, while a value close to 1 represents a high similarity in time-activity patterns and therefore a high synchronization between both partners.

We also computed *S* between each female and all ten males to examine how the synchrony index of a female and its mate compared with the index between her and any other male. We compared the *S* values of females with their actual mates to the *S* values of females with all 10 males using an exact binomial test. Here, the null hypothesis was that the actual mate of a female was as likely as any other male to be the one showing the highest behavioral synchrony with the female.

Descriptive statistics are all given in the form of mean ± standard deviation (SD) with the range in parentheses. All statistical tests were performed in R (v. 4.3.4, R Core Team 2024) with a two-tailed significance level of *a* =

0.05. To compare the overall percentages in time-activity patterns between the sexes, we used the exact Mann-Whitney U test as implemented in the R package coin (Hothorn et al. 2008).

3. Results

3.1 Ethogram

For the ethogram, we described a total of 85 behaviors categorized into ten distinct behavior categories. In total, 1357 quantitative records were obtained. The ethogram included the following behavior categories: *maintenance behaviors* (1. Body shake, 2. Head scratch, 3. Head shake, 4. Tail wag, 5. Wing & leg stretch, 6. Bilateral wing stretch, 7. Yawn, 8. Bill grind, 9. Bill wipe, 10. Touch-foot, 11. Autopreening, 12. Bath), *physiological behaviors* (1. Ruffling, 2. Heat-exposure display, 3. Drink, 4. Food intake, 5. Defecation), *locomotion behaviors* (1. Move, 2. Climb 3. Flying), *inactivity behaviors* (1. Perch, 2. Resting, 3. Roosting), *agonistic behaviors* (1. Neck & head feather raise, 2. Foot-lift, 3. Bill gape, 4. Wing-raise display, 5. Lunge, 6. Bite, 7. Bill fence, 8. Claw, 9. Rush, 10. Flying approach, 11. Flight attack, 12. Fight, 13. Redirected aggression), *displacement behaviors* (1. Displacement preen, 2. Displacement food-intake, 3. Displacement rub, 4. Displacement scratch, 5. Displacement hold-bite, 6. Displacement head down shake, 7. Displacement yawn, 8. Displacement allopreening, 9. Displacement mutual feed, 10. Irritated body shake, 11. Bill clasp), *submission behaviors* (1. Turn away, 2. Slide away, 3. Alert and fear reaction, 4. Apparent death display, 5. Bob, 6. Head-tilt solidarity display, 7. Crouch-quiver solidarity display, 8. Upside-down lift solidarity display 9. Peer, 10. Unison jerk, 11. Singleton jerk), *social behaviors* (1. Contact-sitting, 2. Mutual nibbling, 3. Allopreening, 4. Reciprocal cloacal preen, 5. Non-sexual social play, 6. Begging, 7. Non-sexual Allofeeding), *sexual behaviors* (1. Sexual social play 2. Apparent copulations, 3. Jerk display, 4. Preen display, 5. Scratch display, 6. Rapid turn, 7. Sexual allofeeding 8. Copulation), *behavioral disorders* (1. Erratic flights, 2. Head tilt, 3. Crouch-quiver solidarity display, 4. Upside-down lift solidarity display, 5. Loop-walking, 6. Pterotillomania or feather plucking, 7. Overt allo-preening, 8. Auto-mutilation, 9. Allo-mutilation, 10. Redirected aggression 11. Egg destruction, 12. Infanticide). Fig. 1 & 2 provides some illustrations. Detailed descriptions and methodological details are provided in the Supporting Information (SI).

3.2. Time-activity patterns

Table 1 summarizes the proportion of time spent in all eight main activity categories relevant to the observation period. In all monitored individuals, the predominant activity pattern was inactivity at 49.0 ± 4.9% (40.7–57.9%, Fig. 3), followed by maintenance at 18.1 ± 3.0% (10.5–23.6%), and social behavior at 14.2 ± 2.1% (9.3–16.3%). Physiological behaviors accounted for an average of 8.3 ± 1.8% (5.7–11.5%) and locomotion contributed on average 5.9 ± 1.6% (4.1–8.9%). Intrapair aggressions were only documented in a single pair formed by individuals #59 and #91 during the observation period, but even for this pair, the occurrence of such behavior remained rare and remained the least common of all categorized social behaviors. No significant sex-specific differences were observed for any of the enlisted behavior categories (see Table 1).

The timing of physiological behaviors followed a bimodal pattern (see Fig. 4), with the highest activity observed between 08:00 and 08:59 and another peak between 16:00 and 16:59. These two peaks were thus closely associated with the feeding schedules. Indeed, foraging corresponded to the near totality of time spent displaying physiological behaviors. Inactivity and diurnal resting peaked in many individuals during post-feeding periods (10:00–13:00 and 17:00–19:00). Both agonistic and submission behavior were closely associated with the presence or proximity (i.e., auditory but no visual contact) of the animal keepers. Maintenance behaviors were recorded without any evidence for specific time activity peaks, although auto-preening typically followed prolonged periods of inactivity or allopreening sessions. Locomotion behaviors showed no time specific pattern, and the frequency of movements during a time period appeared to be context dependent. Behavioral disorders occurred either in association with the direct presence of keepers (as an obvious trigger) or had no identifiable visual or acoustic trigger (often the case in chronic forms of stereotypies). Behavioral disorders were observed in eight out of 20 observed individuals.

3.3 Synchrony in time-activity pattern and breeding output

The hierarchical cluster analysis demonstrated the presence of intra-pair synchronization in time-activity patterns, with five out of ten pairs being correctly forecasted as actual pairs (see Fig. 5), and three other pairs (#154/#86 –

#male studbook ID/#female studbook ID, #141/#129 and #79/#54) showed slight divergences but remained within the same cluster. In contrast, two pairs (#15/#132 and #59/#91) showed a higher divergence in their time activity patterns.

Similarly, the synchrony index for each pairing resulted in a comparable trend, with most pairings achieving a S value of > 0.75, except for #79/#54 and #15/#132 (Fig. 6). The distribution of time-activity patterns indicates a high intra-pair synchrony with a mean $\bar{S}$ of 0.78 ± 0.067 across all actual pairs, with an evident overlap between partners in the frequencies and the temporal distribution of the behaviors exhibited (see Fig. 4).

The simulation of the pairings between each female and all possible males revealed that synchrony was always higher with the actual partner than with any other male (exact binomial test, $p < 0.0001$; Fig. 6).

When linking the synchrony index to reproductive performance, it became clear that a threshold of 0.75 seems to be necessary for breeding to occur (Fig. 7). Poor social and behavioral synchrony seemed associated with low reproductive performance (Fig. 7), as the pairings #79/#54 and #15/#132 did not produce eggs and were consequently separated in 2019 or 2020, respectively. The pair #59/#91 did not produce offspring at ACTP, but it sired two offspring in 2017 in Qatar which is compatible with a synchrony index higher than 0.75. An interesting case was the pair #141/#129 which showed the highest synchrony index and produced several clutches, yet none of the eggs were fertile. Both #141 and #129 produced offspring with different partners in 2021 (#141) and 2023 (#129).

Our experience is that established pairs often showed an increase in behavioral synchronization within the first six weeks of pairing, which allowed ACTP staff to assess the pairing success in time before egg laying. Using this information to improve the compatibility between pairs, together with nutritional improvement and environmental enrichment, resulted in a steady increase in offspring numbers at ACTP Germany: 2019 yielded 11 offspring, 2020 yielded 21, 2021 yielded 50. Up to four clutches were laid by each pair, which we restricted to two for the years from 2022 onwards. This yielded 35 offspring in 2022, 42 offspring in 2023 and 44 offspring in 2024. It also increased the numbers of parents capable of successfully raising their chicks from 0 in 2019 & 2020 to 2 in 2021, 3 in 2022, 7 in 2023, and 16 in 2024. There was a similar increase in fertility rates, starting with 39% in 2019, 29% in 2020 when several young pairs laid their first clutch, 45% in 2021, 47% in 2022, 47% in 2023, and 60% in 2024. These results are based on a total of 243 produced clutches recorded (25 in 2019, 48 in 2020, 54 in 2021, 41 in 2022, 43 in 2023 and 32 in 2024) and 86 forced mating attempts conducted during the same time period at ACTP Germany (25 in 2019, 14 in 2020, 16 in 2021, 8 in 2022, 14 in 2023 and 9 in 2024).

4. Discussion

Our main objectives for this study were to (1) describe the full suite of behaviors of Spix's macaws in human care, (2) document their time activity patterns, and (3) investigate the degree of intra-pair synchrony in time activity patterns and its relation to breeding performance. We will now discuss the results in view of potential applications for conservation practices relevant to the management of *ex situ* breeding programs as well as to the reintroduction of parrots in the wild.

Ethological data, behavioral disorders and implications for animal welfare and conservation

Our study provides the first ethogram for the Spix's macaw, comprising a total of 85 behaviors, including stereotypies and other behavioral disorders (hereafter, *behavioral disorders*). These complement ethograms previously published for various Old World and New World parrots, including *Eupsittula canicularis* (Hardy 1963), *Agapornis* spp. (Dilger 1960), *Calyptorhynchus lathami* (Pepper 1996), *Trichoglossus* spp. (Serpell 1979), *Loriculus* spp. (Buckley 1968), *Cyanoramphus* spp. (Higgins 1999), *Nestor notabilis* (Keller 1976), *Cacatua* spp. (Noske *et al.* 1982, Higgins 1999, Rowley 1990), *Amazona* spp. (Levinson 1980, Lantermann 1987, Snyder et al. 1987, Prestes 1991, Queiroz *et al.* 2014) and other neotropical species (Ayres-Peres & da Silva 2017).

Most of the behaviors of Spix's macaw appear to be similar to those recorded for closely related species in both captive and wild environments (Uribe 1982, Christiansen & Pitter 1992, Pitter & Christiansen 1995, 1997, Schneider *et al.* 2006, Favoretto *et al.* 2024). We recorded a total of 12 behavioral disorders. The stereotypies which we classified as physical (6-10 in SI 3.1.9) have also been reported for other parrots (Luescher 2006, Acharya & Rault 2017). For example, feather plucking—a known problem in Spix's macaw populations (Hammer

& Watson 2012)—is ubiquitous in captive stocks (van Zeeland et al. 2009). In contrast, other stereotypical displays we observed are little discussed in the literature (e.g., non-physical stereotypic displays, infanticide), which could imply that some of these behaviors are species-specific, or that they are little studied, or both. While no wild parrot has been documented to exhibit the aforementioned disorders, behaviors we consider here to be disorders in the context of captivity may occur in nature with a different etiology, such as egg destruction and infanticide (see Heinsohn et al. 2011). Such behaviors may occur in the wild in the context of intraspecific or interspecific competition. In our study population, it was exhibited only by some individuals whereas other individuals were never observed to conduct such behavior.

In terms of time activity patterns, resting was the predominant behavior, followed by maintenance and social behavior as observed in other captive parrots such as Scarlet macaws (*Ara macao*, Cornejo *et al.* 2005), Lear's macaws (*Anodorhynchus leari,* de Azevedo *et al*. 2016), Hyacinth macaws (*Anodorhynchus hyacinthinus*, Checon *et al*. 2020), Vinaceous-breasted amazons (*Amazona vinacea*, Ramos *et al.* 2020) or Senegal parrots (*Poicephalus senegalus*; Lantermann 1998). While there is no such data for wild Spix's macaws, studies on other species suggest that prolonged period of inactivity is a hallmark of captivity. For example, around a year after their release, Scarlet macaws spent 35% of their time resting compared with 41% for conspecifics in human care (Cornejo *et al.* 2005).

We recorded Spix's macaws to spend 8.3 ± 1.8% (5.7-12.4) of their full diurnal activity period foraging, which is lower than the value of 15% reported for captive Scarlet macaws (Cornejo *et al.* 2005), but comparable to estimates provided for Hyacinth, Scarlet and Military macaws (*Ara militaris*) from the Loro Parque Zoo (Britsch 2018). Although foraging activities vary markedly between individuals and environments, foraging activities were reduced in captivity. In their natural environment, parrots spent a substantial amount of time foraging as demonstrated for released Scarlet macaws (28%; Cornejo *et al.* 2005), wild Ouvéa parakeets (*Eunymphicus uvaeensis*) (47%; Robinet *et al.* 2003), or wild Glossy black cockatoos (*Calyptorhynchus lathami halmaturinus*) on Kangaroo Island (26% for non-breeding, 36% for breeding birds; Chapman & Paton 2005). Such divergence between wild and captive birds is expected, considering that foraging activities include search flights to locate feeding sites, the handling of food items, and interactions with competitors for access to resources (Chapman & Paton 2005, Brightsmith *et al*. 2018). While comparative data for locomotion are scarce, we observed Spix's macaws to spend even less time actively moving than foraging, which is also likely a response to easy access to food and the captive environment.

By eliminating some constraints such as unpredictable food distribution and occurrence, competition, and predation, conditions in human care induce a shift in activity patterns which may promote the expression of behavioral disorders. Compared to its (presumed) absence in the wild, we observed Spix's macaws to spend on average 3.2% of their full diurnal activity period exhibiting behavioral disorders. The time budget dedicated to such behaviors varied a lot between individuals—from being completely absent in some individuals to reaching up to three hours per day for one individual (#15). The exact etiology of behavioral disorders remains unclear. In ACTP's captive population, it probably results from the lack of some activities, possibly the lack of social interactions and environmental challenges, in conjunction with stress factors resulting from husbandry conditions initially suboptimal. The latter comprises inappropriate hand-rearing, lack of enrichment, and poor health management, but other intrinsic factors may also play a role, such as personality, stress levels, or genetics (see Garner *et al*. 2006, Luescher 2006, Owen & Lane 2006, Cussen & Mench 2015).

Reducing the occurrence of behavioral disorders through the optimization of husbandry protocols is an important way to promote animal welfare and the productivity of *ex situ* populations. This is because such behaviors can lead to physical injuries by auto-mutilation, redirected aggression, and/or feather plucking (Owen & Lane 2006, Luescher 2006, Acharya & Rault 2020). Behavioral disorders in captive parrots can also interfere with breeding. As an extreme illustration, ACTP staff observed a few females purposefully destroying their eggs during the incubation period or killing their offspring after hatching.

Husbandry should therefore aim at creating an environment that minimize the occurrence of behavioral disorders (Coulton *et al*. 1997, Field & Thomas 2000, Meehan *et al*. 2004, Wang *et al*. 2009, van Zeeland *et al*. 2013, Reimer *et al*. 2016, Rodriguez-Lopez 2016, de Almeida *et al.* 2018, Livingstone 2018). For this purpose, behavioral data serves as an important template to improve husbandry guidelines. Several measures were taken to reduce behavioral disorders in ACTP facilities following data collection and analysis. For example, the environment of all birds has been frequently enriched since the behavioral data collection for this study was completed by providing them with paper rolls, cardboards, new modular toys, treating dispenser toys and fresh greens. ACTP staff has also progressively favored the rearing of chicks by their parents. We have yet to investigate and disentangle the effects of such changes on time-activity patterns, but behavioral disorders in ACTP facilities have substantially dropped over time. We assume that minimizing the occurrence of behavioral disorders will improve the success of conservation breeding and the success of reintroducing animals to the wild. Indeed, the expression of behavioral disorders could impede the individual's ability to respond to environmental changes adequately and limit the capacity to learn or develop behavioral strategies important for survival. In addition to genetic criteria (inbreeding, relatedness) and the physical condition of the bird, the expression of some behaviors as categorized here were used to select candidates for reintroduction—retaining only those showing no evidence of behavioral disorders. The first two cohorts selected in such a way were therefore released in the wild in June and December 2022 and the first wild-born offspring successfully fledged in May 2024 (Purchase *et al*. 2024, Vercillo *et al*. 2024). While these results are encouraging, more efforts could be directed at bringing behavioral profiles of captive birds closer to that of wild ones. For example, the time-activity pattern of wild psittacines is influenced by temporal changes (e.g., Chapman & Paton 2005), so modifying the captive environment to induce similar changes could be beneficial.

Behavioral synchrony and implications for conservation breeding efficiency

Another way to increase the productivity of animals in captivity is to provide individuals with partners with which they are willing to mate (Martin-Wintle et al. 2015, et al. 2019, Alverson et al. 2023). This can be achieved in three main ways. One solution is to let animals freely choose their partners as they would do in the wild. Free mate choice has indeed been linked to higher breeding output in psittacines (Waugh & Romero 2000, Luescher 2006, Spoon *et al*. 2007), mammals (Parrott *et al*. 2019) and reptiles (Lemm & Martin 2023). Letting animals choose their mates freely is usually not feasible in captivity because of time and space constraints, or because of limited availability of candidate partners. Moreover, free mate choice may not always result in the desired conservation outcome of maintaining high genetic diversity. A second possibility is to expose, in a controlled setting where actual copulation is impossible, a focal individual to a few candidate mates so as to infer mate preferences through the recording of its behavioral response. While this has proved successful in some species (Martin-Wintle et al. 2015, Alverson et al. 2023), assessing mate preferences in such a way requires a large and very specific layout for the enclosures. Finally, breeders may also adjust pairings based on observed behavioral compatibility (Spoon *et al*. 2007, Fox and Millam 2014). Breeders tend to consider members of pairs which spend a lot of time together as "harmonious pairs" and a harbinger of good productivity. Indirect evidence suggests that the empirical knowledge of breeders may be correct. For example, in cockatiels (*Nymphicus hollandicus*), more eggs were laid, more chicks hatched and reared by pairs which had a "higher cohesion and synchrony", exhibited frequent allopreening and lower aggression (Spoon *et al*. 2007). Raw data of behavior could therefore be helpful to evaluate intra-pair "harmony" to forecast the chance of successful breeding. These observations suggest that letting individuals express their mate preferences can improve breeding output. Unfortunately, how such behavioral compatibility is assessed in practice by breeders when mate choice is constrained has been little explored. Our approach was to design a synchrony metric (*S*) to compare the time activity patterns of each paired individual and to test whether such a metric predicted breeding performance.

Our results show that there seems to be a threshold of synchrony ($S = 0.75$) below which pairs had a low number of eggs and offspring. One pair proved to be an exception (#141/#129) in terms of fertility. While the pair #141/#129 produced many eggs, no offspring resulted from them. A pathological cause seems unlikely, as both #141 and #129 produced offspring with different partners later on. A poor genetic match leading to the expression of lethal alleles might be a possible explanation, given that the entire population is highly inbred and based on six founder individuals only (Purchase 2019). The pair #59/#91 did not produce offspring at ACTP Germany, although it sired two offspring in 2017 in a facility in Al Wabra Wildlife Preservation, Qatar (#216 and #217, Purchase 2019). Whenever breeding programs rely on forced pairings, the breeding output may thus be improved by selecting candidate mates using behavioral data such as behavioral profiles and time-activity patterns in addition to other criteria that may be employed, including age, genetics, and the results of the previous breeding success. Our sample size was, however, arguably small, and further data should be collected in Spix's macaws and in other species to assess the usefulness of the synchrony index in practice. Another open question is then, when does measuring synchrony provide the best forecast? It seems tempting and practical to monitor behaviors and measure synchrony in time-activity patterns before pairings. However, we observed that in poorly synchronized pairs females still showed the highest synchrony with their actual partner in comparison with other candidates. This highlights that synchrony in time-activity patterns is a variable likely to be influenced by the social environment. The Spix's macaw is a gregarious species and tends to form temporary bonds and flocks with conspecifics, aligning their behavior within their social flock (see Hobson *et al*. 2014). Even in forced pairings that result in no sexual activity, the birds engage in social tolerance and interactions, leading to an increase in synchrony.

There is still no data available to establish whether a measure of synchrony before pairing could forecast breeding output. Our experience is that established pairs often show an increase in behavioral synchronization within the first six weeks of pairing, which allowed ACTP staff to assess the pairing success in time before egg laying. Whenever they detect poor synchrony, ACTP staff thus either swapped pairs immediately when the synchrony was really low, or else during the onset of the next breeding season. This approach has been effective as it helped ACTP staff to reevaluate and adjust >90% of all pairings between 2019 and 2024 which had either never bred or usually produced infertile clutches. To increase breeding performance even further, groups of six juveniles (3 males and 3 females with low relatedness) have been placed together in enriched and enlarged aviaries since 2023. This allowed them to live together until they freely choose their partner, which occurred around 3 yrs old. After this age, which coincides with the appearance of territorial behavior, the current plan is to place each pair in a separate breeding aviary. The future will show whether this is the appropriate way forward.

5. Conclusions

Our study highlights that the detailed monitoring of behavior in ongoing or planned *ex situ* programs is paramount, especially in socially complex species such as the Spix's macaw and many other parrots. Behavioral studies can help measure welfare issues in terms of stereotypies and other behavioral disturbances and displacement behavior and improve husbandry guidelines to increase the effectiveness of *ex situ* breeding programs. The discovery of behavioral disorders and of prolonged periods of inactivity among Spix's macaws in human care within the facility of ACTP Germany prompted them to enrich the environment and modify breeding protocols. The finding that behavioral synchrony among paired individuals is a reliable predictor of breeding performance also prompted them to revise the procedures for matching partners based on behavioral criteria. We documented here how breeding productivity improved as a result of such changes. Importantly, the relevance of behavioral monitoring extends beyond the management of *ex situ* breeding programs. Characterizing the behavior of individuals is also key to select candidates to be released in the wild and to improve the success of reintroduction programs. Ethograms are a necessary requirement to check whether selected birds successfully adjust to their novel environment (see Purchase *et al*. 2024, Vercillo *et al*. 2024). While behavior is not the only factor determining animal welfare and breeding productivity, considering this information is decisive to improve conservation breeding in practice. We would like to end by urging others to participate in the global effort of integrating behavioral studies into conservation science (Curio 1996, Buchholz 2007, Berger-Tal & Saltz 2016, Snijders et al. 2017).

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Tables

Table 1 – Summary of activity patterns observed for 20 adult Spix's macaws and test statistics for the comparison of males and females (exact Mann-Whitney U test). Values for single study groups (combined, male and female) are given as the percentage of the diurnal period spent on each focal activity.

Behavior category	combined *n* = 20	males *n* = 10	females *n* = 10	z-Score	*p*-value
maintenance	18.11 ± 2.96 (10.50-23.57)	18.22 ± 3.37 (10.50-23.57)	17.99 ± 2.68 (13.75-22.15)	0.33	0.739
physiological	8.34 ± 1.81 (5.67-11.48)	8.36 ± 1.85 (6.10-11.48)	8.31 ± 1.86 (5.67-11.32)	0.254	0.846
social	14.24 ± 2.07 (9.25-16.33)	**	**		
agonistic	0.58 ± 0.23 (0.33-1.16)	0.59 ± 0.24 (0.33-1.16)	0.57 ± 0.24 (0.33-1.09)	0.22	0.818
inactivity	49.02 ± 4.87 (40.67-57.88)	48.20 ± 4.47 (40.67-54.52)	49.83 ± 5.36 (40.81-57.88)	-0.78	0.436
submission	0.67 ± 0.51 (0.04-1.92)	0.67 ± 0.45 (0.04-1.54)	0.67 ± 0.59 (0.21-1.92)	0.41	0.684
behavioral disorders*	3.19 ± 4.56 (0-18.45)	3.77 ± 5.77 (0-18.45)	2.61 ± 3.14 (0-8.39)	-0.31	0.754
locomotion	5.86 ± 1.64 (4.08-8.89)	5.92 ± 1.71 (4.08-8.80)	5.79 ± 1.66 (4.26-8.89)	-0.11	0.918

* in individuals where no stereotypic behavior was observed the relative frequency was considered as 0.

** social interactions involved both male and female and are therefore identical for both genders.

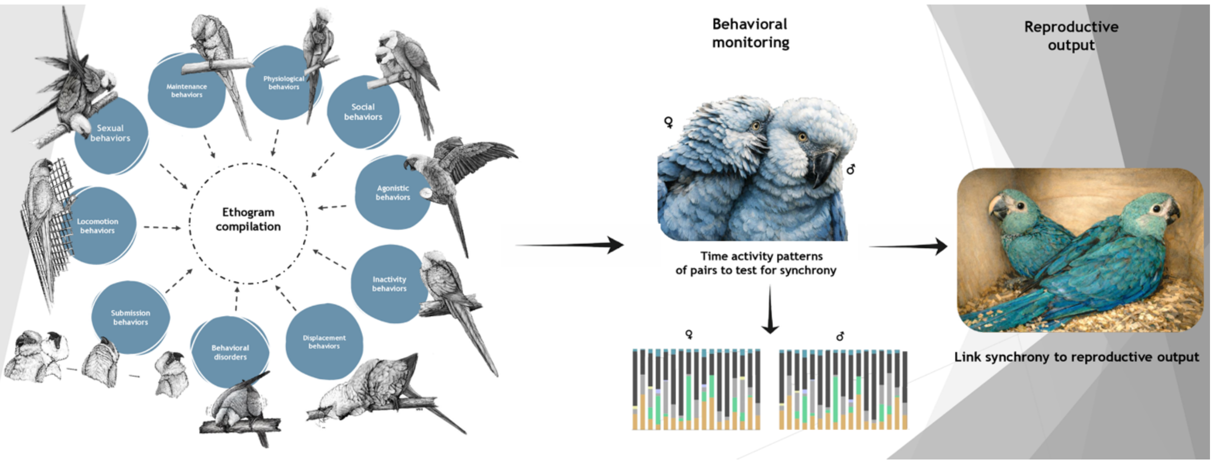


Figure 1 – Graphical abstract with the associated behavior categories featuring each characteristic behavior of the respective category. The time activity patterns were compiled using some of the mentioned behavioral categories (illustrations by V. M.). Illustrations for agonistic and submission behavior adapted from Marcuk *et al*. 2020. Illustration of pair based on a picture from K.S.

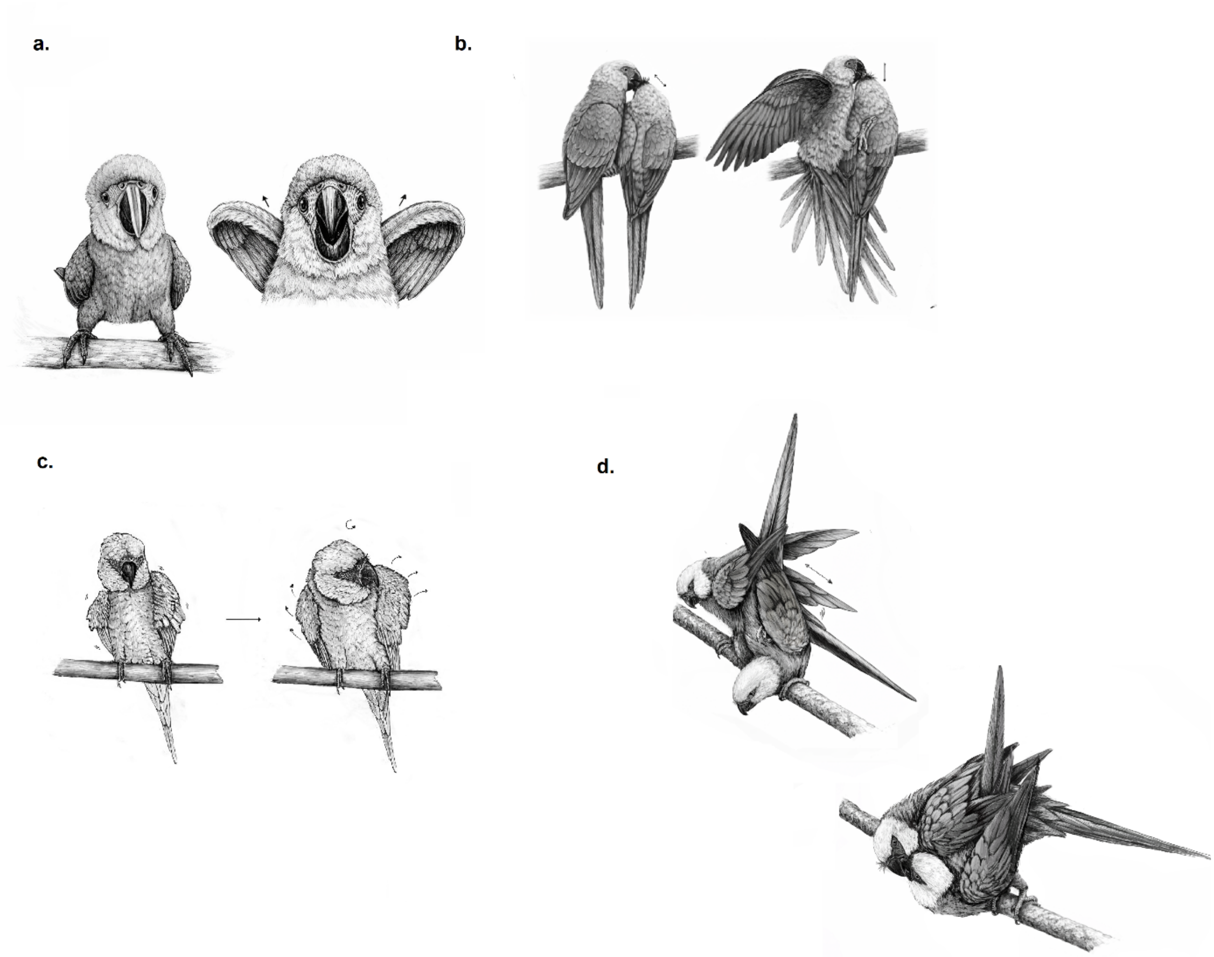


Figure 2 – Sample of illustrations of different behaviors: a.) begging b.) sexual allofeeding c.) body shake and d.) active phase of a copulation. The complete ethogram is provided in SI.

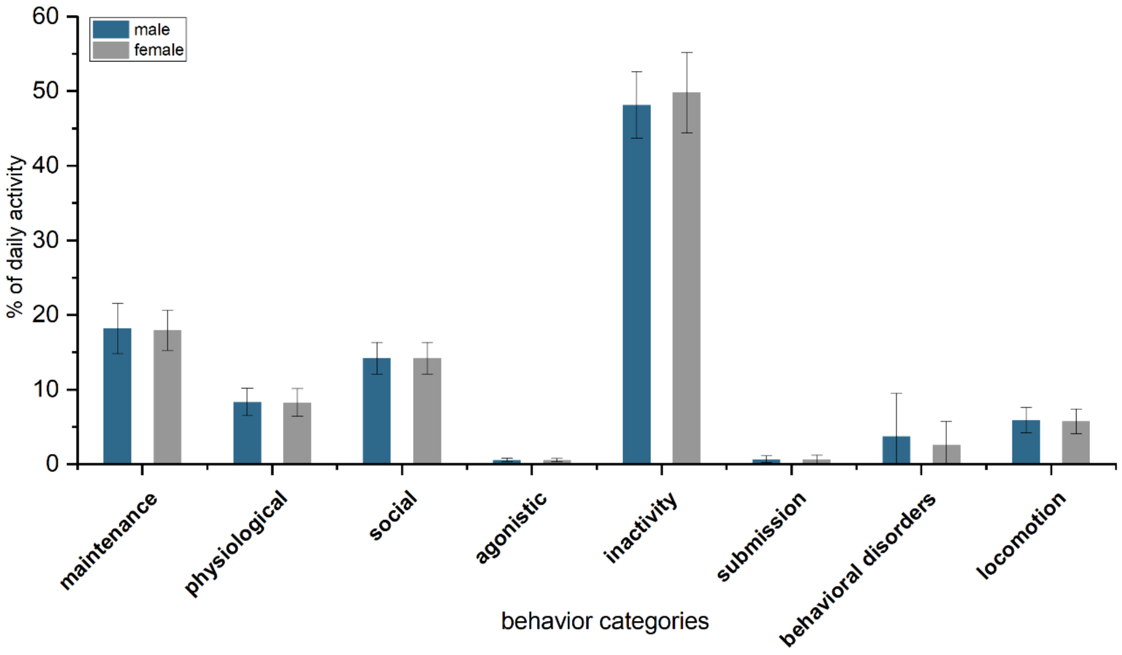
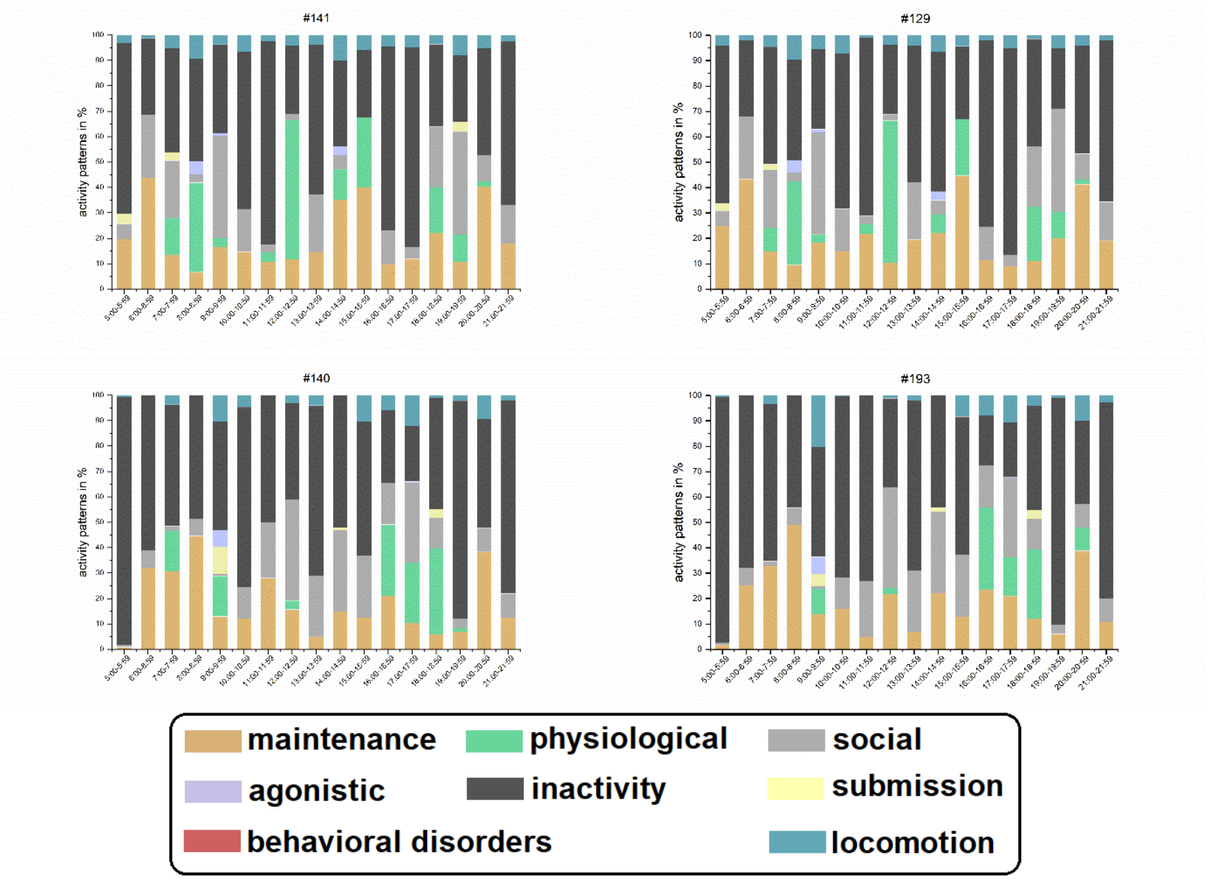
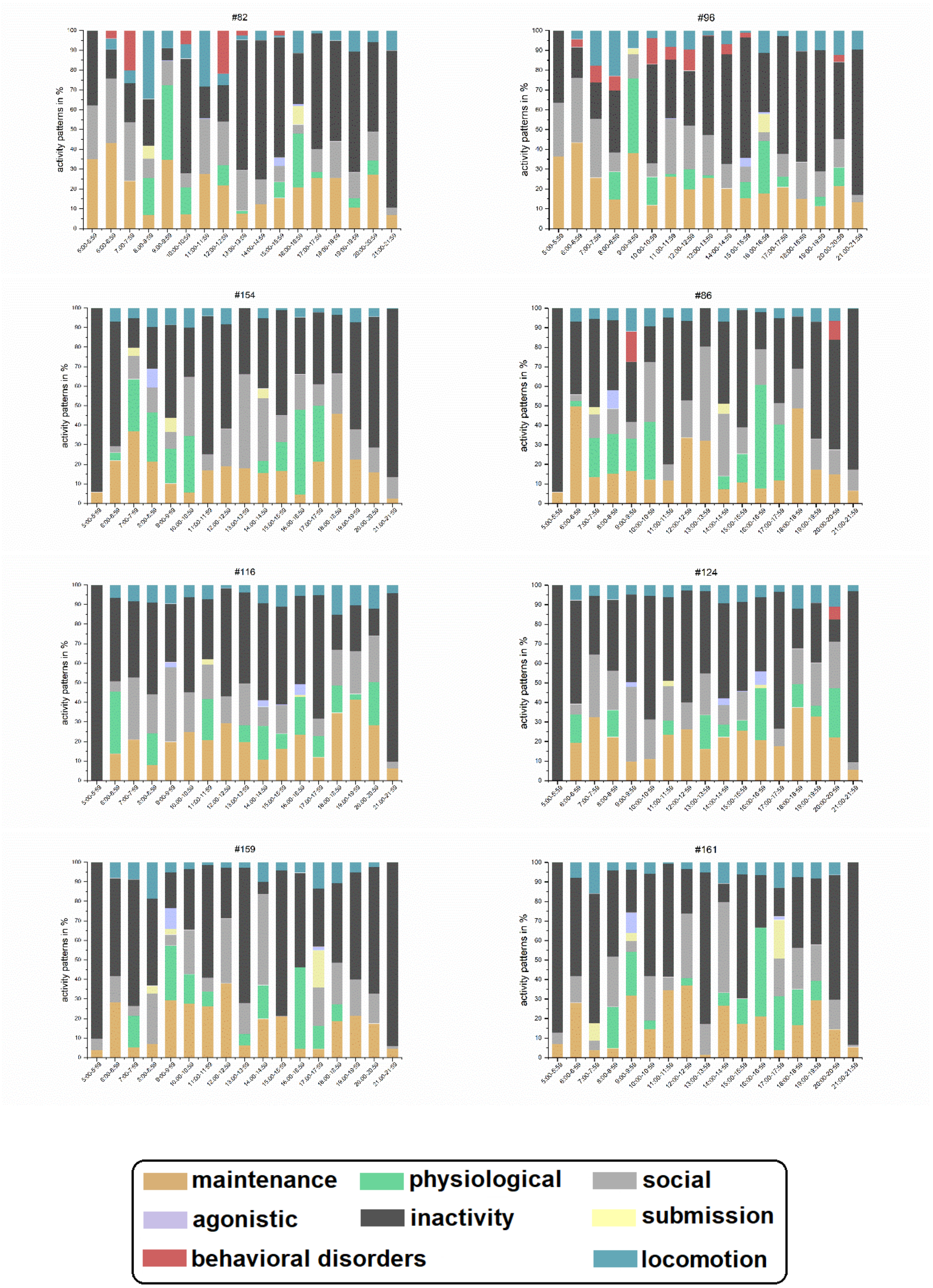


Figure 3 – Time activity budgets of the Spix's macaw under captive conditions, male (blue) and female (grey).




#82
#96
#154
#86
#116
#124
#159
#161
activity patterns in %
0
10
20
30
40
50
60
70
80
90
100
5:00-5:59
6:00-6:59
7:00-7:59
8:00-8:59
9:00-9:59
10:00-10:59
11:00-11:59
12:00-12:59
13:00-13:59
14:00-14:59
15:00-15:59
16:00-16:59
17:00-17:59
18:00-18:59
19:00-19:59
20:00-20:59
21:00-21:59
maintenance
physiological
social
agonistic
inactivity
submission
behavioral disorders
locomotion

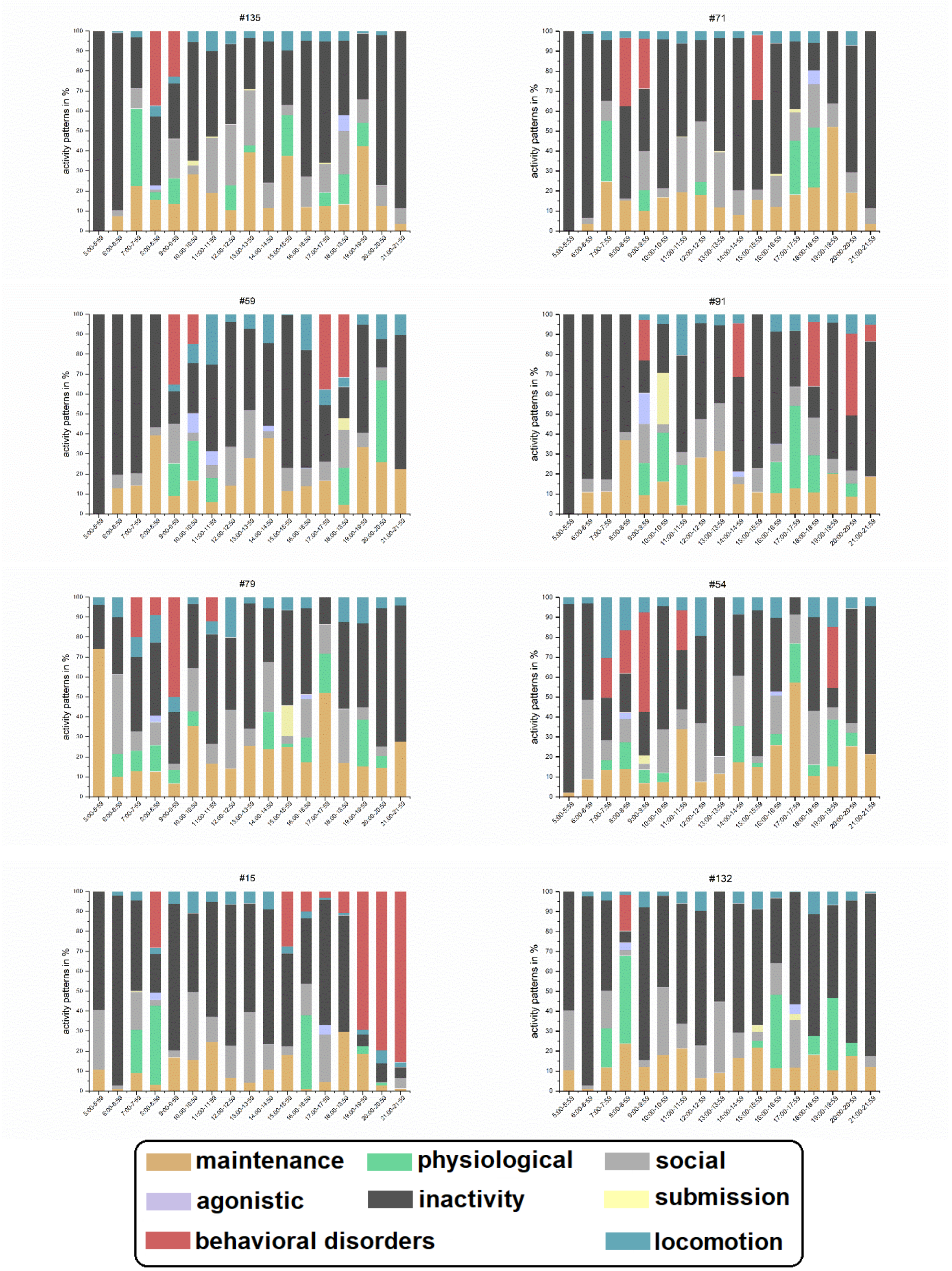


Figure 4 – Diurnal activity patterns of 20 individuals with associated studbook numbers, with each row representing a pair with the male on the left and the female on the right side. Pairs are sorted by decreasing values of intra-pair synchrony as measured by the metric *S*. Each row represents one pair. Stacked column bars are presented for males on the left and for females of each pair on the right side, respectively.

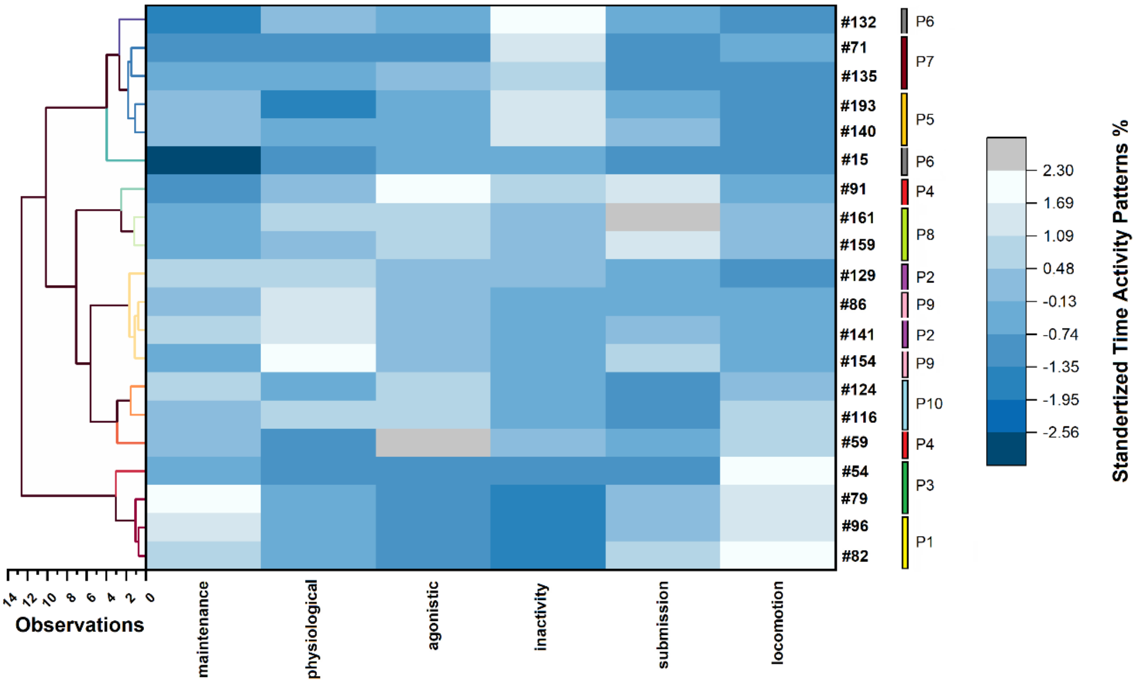


Figure 5 – Heatmap with a hierarchical cluster analysis using standardized data (type = Ward, average type = Euclidean, k = 10 clusters), actual pairs are highlighted (P1-P10) with the associated Studbook numbers, clusters are showing the associated individuals with the highest inter-individual similarity. Pairings (with respective male/female) P1: #82/#96, P2: #141/#129, P3: #79/#54, P4: #59/#91, P5: #140/#193, P6: #15/#132, P7: #135/#71, P8: #159/#161, P9: #154/#86, P10: #116/#124.

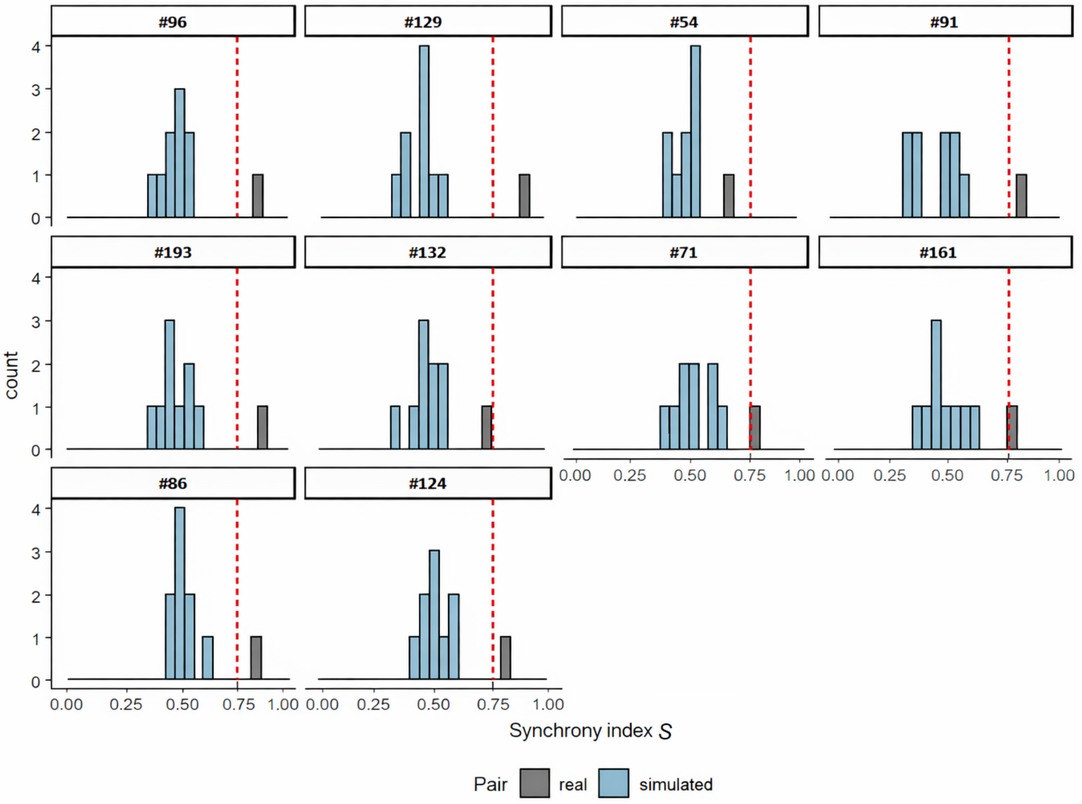


Figure 6 – Synchrony indices presented for each female, showing the calculated synchrony index for the actual "real" partner in grey (■) and the simulated partners in blue (■). The studbook numbers of the females are indicated above each plot. Threshold of $S = 0.75$ is indicated by the red dashed line (---).

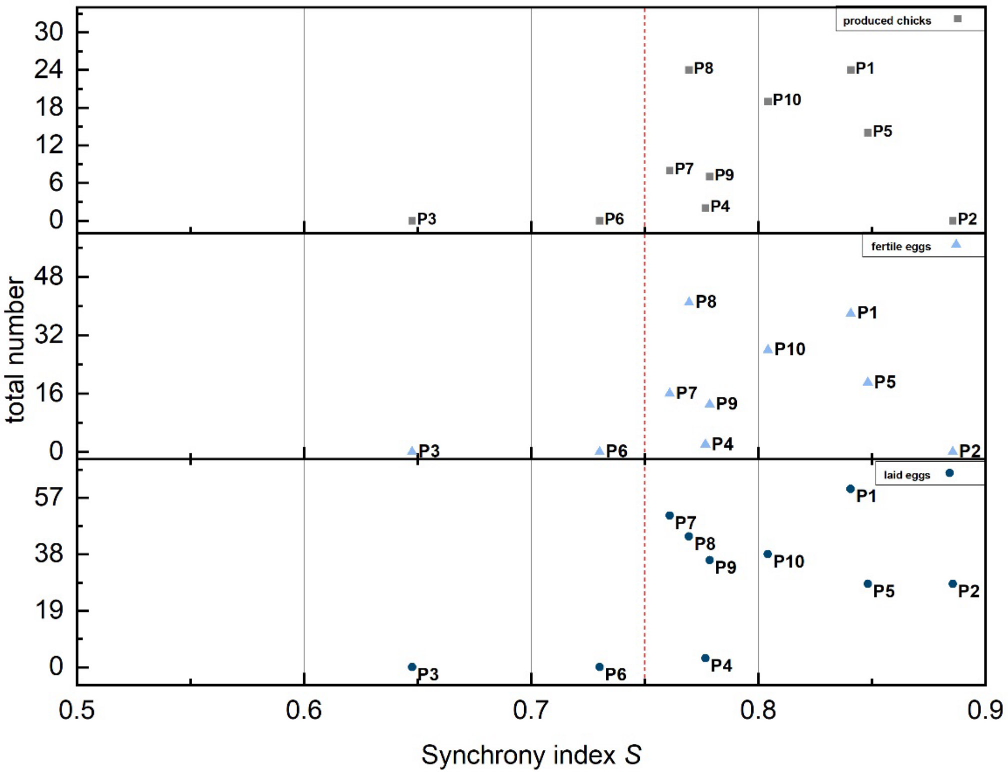


Figure 7 – Scatter plot to illustrate the relationship between Synchrony index (S) of the observed ten pairings and the total number of laid eggs (●), fertile eggs (▲) and chicks (■) produced between 2018–2023. The red dashed line (---) indicates the threshold of $S = 0.75$. The IDs of individuals forming the respective pairs are provided in the legend of Fig. 5.