How monitoring behavior can inform conservation? The case of Spix's macaws under human care

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Abstract: The Spix's macaw (*Cyanopsitta spixii*), a Brazilian endemic psittacine formerly native to the north-eastern part of Bahia state has been classified as extinct in the wild since 2019. The entire ex-situ breeding population is currently managed by program-associated holders in Germany, Brazil and Belgium. Breeding efforts increased the global population under human care from a historical low of 53 individuals in 2000 to 364 individuals as of January 2025. The first two cohorts were released in the wild in June and December 2022 and the first wild-born offspring fledged successfully in May 2024. As part of the pre-release program, we studied the behavior of 123 birds in 2018-2019 within the German facility of the Association for the Conservation of Threatened Parrots e. V. (ACTP) with the goal to optimize general husbandry practices as well as pre-release and post-release protocols. We compiled an ethogram consisting of 75 non-sexual behaviors, monitored the time activity patterns of ten pairs during the daytime period, and analyzed the breeding output between 2014 and 2024. Our results reveal that the time activity patterns were relatively consistent across individuals. Nonetheless, each female was more in synchrony with its mate than with any other male. Moreover, breeding readiness and breeding success were strongly influenced by the synchronicity of the pairs. We discuss how the conservation of monogamous parrots could benefit from behavioral monitoring, drawing insights from the historical improvements in the reduction of behavioral disorders and in the increase in breeding success of the Spix's macaw.

Keywords: *Cyanopsitta spixii*, ethogram, extinct in the wild, pair formation, stereotypies, synchronicity, 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). The oldest record of the species was made by Johann Baptist von Spix about 200 years ago. The species was then 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). Only in the late 20th century, 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). While a single male was discovered in the wild near Riacho Melância later in July 1990, no remnant females were present. In 1995, one female was thus released into the wild, but the reintroduction attempt failed, as the individual died shortly after its release (Juniper 2004). The last male was never seen again after October 2000, leading to the reclassification 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 2004). From an initial captive population size of 53 individuals by December 2000 (Purchase 2019), continuous efforts contributed to the growth of the population to 364 individuals as of January 2025. However, while the reproductive output of the species is consistently improving, little has been published about the behavior, ecology, breeding biology and demography of the species.

Behavioral data is however crucial, not only for establishing adequate husbandry manuals (Luescher 2006), but also to optimize reintroduction programs (Plair et al. 2008, Azevedo et al. 2017). Importantly, one should seek to avoid the manifestation of stereotypies, which is an issue of animal welfare but is also likely to affect the competence of individuals when they are released into the wild. A wide range of behavioral research has been performed on psittacines over the past decades; ranging from descriptive ethology (Dilger 1960, Hardy 1963, Buckley 1968, Serpell 1971, Levinson 1980, Uribe 1982, Lantermann 1987, Rowley 1990, Prestes 1991, Schneider *et al*. 2006, Favoretto *et al*. 2024) to studies testing specific hypotheses or complex behavior paradigms (cognitive behavior, communication, effects of environmental enrichment or behavioral models; Pepperberg 2000, Dahlin & Wright 2007, Auersperg & von Bayern 2019, Checon *et al*. 2020, Ramos *et al*. 2020). This research has led to the compilation of ethograms for various Old World and New World parrots: *Eupsittula canicularis* (Hardy 1963), *Agapornis* spp. (Dilger 1960), *Calyptorhynchus lathami* (Pepper 1996), *Trichoglossus* spp. (Serpell 1971), *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, Prestes 1991, Queiroz *et al.* 2014) and other neotropical species (Ayres-Peres & da Silva 2017). In macaws, detailed descriptive work has only been done for the Blue-winged macaw (*Primolius maracana*; Barros 2001, in the wild) or larger species like the Scarlet Macaw (*Ara macao*, Uribe 1982), Blue-and-gold macaw (*A. ararauna*; Uribe 1982), Lear's and Hyacinth Macaw (*Anodorhynchus leari* and *A. hyacinthinus*, respectively, Schneider *et al*. 2006, Favoretto *et al*. 2024) and Red-fronted macaw (*A. rubrogenys,* Christiansen & Pitter 1992, Pitter & Christiansen 1995, 1997; in the wild). In summary, the behaviors of many New World Parrots remain little investigated, reducing the scope for improvements in conservation breeding. The first aim of this study is thus to provide a complete overview of non-sexual behaviors in Spix's Macaws, including stereotypies and other behavioral disorders.

Characterizing when the different behaviors take place (i.e., time activity patterns) is also relevant for improving husbandry conditions in view of successful reintroductions. Time-activity patterns differ substantially between conspecific individuals from in-situ and ex-situ populations (Cornejo *et al.* 2005). The lack of environmental or social interactions and easy access to food often induces a shift in time activity patterns for parrots under human care. Most previous studies indicate that such birds spend predominantly their time resting or performing maintenance behaviors (Lantermann 1998, Cornejo *et al.* 2005, 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 the barred environment are serious concerns as they may be linked to the emergence of behavioral disorders (Meehan et al. 2004, Garner et al. 2006). The second goal of this study is therefore to establish a baseline of the time-activity patterns in Spix's Macaws under standard husbandry conditions. This will allow assessing the performances of alternative enrichment protocols and help identifying how to most efficiently bring time activity patterns of individuals under human care to become as close as possible to those of wild parrots. This along with other factors will be important to promote survival of Spix's macaws after release, and the same applies to other endangered 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 pure genetic criteria are not always particularly successful. In several psittacine species, such pairing designs can trigger redirected aggression or be associated with low breeding success (Waugh & Romero 2000, Luescher 2006). The Spix's Macaw is no exception and, once artificial insemination was discontinued in 2018, optimal genetic matching often resulted in infertile clutches or in individuals not showing any interest in breeding (see Results). Among the community of people breeding parrots, it is generally believed that behavioral compatibility is crucial for breeding success and that a high level of synchronicity among partners is desirable. Unfortunately, there is limited scientific information available about how the behavior of parrots relates to their breeding success. If that link were strong, time activity patterns would have the potential to be used to guide ex-situ breeding and complement genetic choice criterion already in use. Our third and final goal is therefore to assess the relevance of synchronicity in time activity patterns between paired males and females by studying the relationship between synchronicity and breeding output.

To achieve our three objectives, we recorded the behavior of 123 Spix's Macaws in the largest ex-situ population in the world and studied diurnal time activity patterns and behavioral synchronicity of ten breeding pairs outside the breeding season (September-February).

2. Materials and Methods

2.1 Husbandry

The study took place in the facility of the Association for the Conservation of Threatened Parrots e. V. (ACTP), where all Spix's macaws are housed as pairs (adults) or in flocks (immature birds) in partly isolated units. Each unit consists of 12 or 13 aviaries, which are 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 maintain auditory contact with each other. The separation into subunits thus decreases the time individuals spend engaging in activities related to territorial defense.

Each aviary has an indoor and outdoor enclosure, with dimensions of 2 x 3.5 x 2.8 m and 16.0 x 2.0 x 3.0 m (length x width x height), respectively. The indoor aviary is heated to 18 – 21 °C from October-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 is covered with a 2-3 cm thick layer of wood shavings. Each box is equipped with two high-definition cameras (Vicon V988D-W311MIR Dome Camera): one indoor 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.

The inventory of the outdoor enclosure consists of an individual constellation of perches and a canopy (1 m), which protects the birds from direct sun exposure or excessive rain. An artificial rain system is installed in all outdoor aviaries, which is operated on automated schedule over the warmer months (April-September).

All birds are fed twice daily (8:00-9:00 am and 3:30-4:30 pm) and supplied with additional pellets during the breeding season lasting from March-August. Food quantity is adjusted in the winter and a maintenance diet for adults is implemented to counteract excessive weight gain and ensure the maintenance of birds close to desired weights (female: 288 g, male: 318 g, average weights of *n* = 112; unpubl. info.) during both semi-annual periods (breeding and nonbreeding). Water is provided *ad libitum*. At the beginning of the breeding season, the amount of food is increased, and vitamins and minerals are added. Further changes are implemented if pairs begin to rear chicks.

2.2 Observation methods

Non-contact observations were carried out using cameras, to avoid behavioral changes influenced by the presence of an observer near the aviary. We analyzed the full length of each video recording at a fixed 60-minute interval for the total active daytime period (see above). In total 320 hours of video material were analyzed for the establishment of the behavioral repertoire and quantification of the time-activity patterns. The video sequences were stored externally (AVI format) and analyzed with Avidemux (v. 2.7.4). Based on observations, behaviors were categorized in nine distinct categories (Fig. 1), which are described in detail in the supplementary material, including maintenance (all behaviors included in SI 3.1.1, behavior 1 to 12), foraging (part of the physiological behaviors, see SI 3.1.2, behavior 3 and 4), locomotion (active forms; behavior 1 to 3, SI 3.1.3), resting (SI 3.14, behavior 1 to 4, inactivity), agonistic (SI 3.1.5, behavior 1 to 12, according to Marcuk *et al.* 2020), displacement behavior (SI 3.1.6: behavior 1 to 11, according to Marcuk *et al.* 2020), submission behavior (SI 3.1.7: behavior 1 to 11, according to Marcuk *et al.* 2020), social behavior (SI 3.1.8: behavior 1 to 4, non-breeding) and stereotypies and other behavioral disorders (SI 3.1.9, behavior 1 to 12).

The behaviors of each individual were analyzed during the full diurnal period (from 5:00 am to 9:00 pm, light hours). Time activity patterns were recorded for ten pairs, where the behavior duration (sec) was analyzed for each hour rounded to the second and assigned to the respective behavior category. Displacement behaviors were lumped together with submission or agonistic behavior due to their very short duration. 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 clearly assign records to individuals with no ambiguity (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 boxes had open nests, ensuring that none of the pairs included in this study showed signs of breeding readiness. 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 (min age = 4 yrs). The observation period 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 was collected between 2014-2024 for each breeding pair. 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 candled at least once to determine if an embryo was developing (fertile) or not (infertile). We also counted the total number of offspring once they were weaned.

2.3 Data analysis and statistics

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 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 implemented in the R package coin (Hothorn et al. 2008).

To assess behavioral synchronicity, we excluded displacement behaviors as was the case for time-activity patterns. We also excluded social behaviors since they correspond to interactions and thus, always necessarily occur in synchrony. We finally excluded behavioral disorders since mates were never observed to mirror such behaviors. Using this data, we first performed a hierarchical cluster analysis (type = Ward, average type = Euclidean, k = 10 clusters equal the ten pairings) to determine if the actual pairings clustered based on their temporal behavioral characteristics. The clustering and its representation were compiled using OriginLab 2024a (OriginLab Corporation, Northampton, MA 01060 US). Second, we computed a synchronicity index for each single pair to quantify the observed similarity in time activity patterns. The synchronicity index S is defined as the sum of absolute differences between the relative frequencies across all retained behaviors for each hour ($\text{hour}_1 \ldots \text{hour}_{17}$) of the male ($m$) and of the female ($f$), i.e., as:

$$S = \sum\nolimits_h \sum\nolimits_b \left| \frac{d_{hb\text{♂}} - d_{hb\text{♀}}}{H \times 60} \right| \qquad (1)$$

where h is the index of each hourly period between 5:00:00 and 21:59:59 (i.e., 5:00:00-5:59:59, 6:00:00-6:59:59, ..., 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 (i.e., here 17).

A synchronicity index of 0 represents the highest conceivable divergence of the time activity behavior patterns between female and male, whereas a value close to 1 represents the highest conceivable similarity in behavioral patterns and therefore a high synchronization between both partners.

In addition, we computed S between each female and all ten males to show how S differed between a female and its partner, as compared to how it differed between a female 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. For this test, we considered as the null hypothesis that the actual mate of a female was as likely as any other male to be the one showing the highest behavioral synchronicity with the female.

3. Results

3.1 Ethogram

For the ethogram, we described in total 75 behaviors categorized in nine distinct behavior categories, including Maintenance behaviors (1. Body shake, 2. 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. Auto-preen, 12. Bath), Physiological behaviors (1. Ruffling, 2. Heat-exposure display, 3. Drink, 4. Food intake, 5. Defecation), Locomotion (1. Move, 2. Climb 3. Flying), Resting or inactivity behaviors (1. Perch, 2. Resting, 3. Roosting), Agonistic behaviors (based on Marcuk et al. 2020: 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 (based on Marcuk et al. 2020: 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 (based on Marcuk et al. 2020: 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 behavior (1. Contact-sitting, 2. Mutual nibbling, 3. Allo-preening, 4. Reciprocal cloacal preening), Behavioral Disorders (Non-physical stereotypies or displays 1. Erratic flights, 2. Head tilt, 3. Crouch-quiver solidarity display, 4. Upside-down lift solidarity display, 5. Loop-walking, Physical adverse behaviors: 6. Pterotillomania or feather plucking, 7. Overt allo-preening, 8. Auto-mutilation, 9. Allo-mutilation, 10. Redirected aggression 11. Egg destruction, 12. Infanticide). Detailed descriptions and methodological details are provided in Supporting Information (SI).

3.2. Time activity patterns

The proportion of time spent in all eight main activity categories during the total active diurnal period is given in Table 1. In all monitored individuals, the predominant activity pattern was resting 49.01 ± 4.87% (40.67-57.88 %, Fig. 2), followed by maintenance; 18.11 ± 2.96 % (10.50-23.57 %), and social behavior; 14.24 ± 2.07% (9.25-16.33 %). Foraging accounted for an average of 8.33 ± 1.81% (5.66-11.47%) and locomotion contributed to average 5.85 ± 1.64% (4.08-8.89 %). 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 foraging activities habitually followed a bimodal pattern (see Fig. 3), with the highest food intake activity observed between 8:00 and 8:59 and another peak in food intake activity occurring between 16:00 and 16:59, which was closely associated with the feeding schedules. Inactivity and diurnal resting peaked in many individuals during the 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 frames, however, auto-preening typically followed prolonged periods of inactivity or allopreening sessions. Locomotion showed no time specific patterns and the frequency of movements occurring during a time-period seem context-dependent. Contrary to agonistic and submission behaviors, behavioral disorders occurred either in association with the direct presence of keepers (with 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 Synchronicity in time-activity pattern, with implication to the breeding output

The hierarchical cluster analysis demonstrates the presence of intra-pair synchronization in the time-activity patterns, with five out of ten pairs being correctly forecasted to the actual pairing (see Fig. 4), 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 higher divergence in their time activity patterns. Similarly, the synchronicity index for each pairing resulted in a comparable trend, with most pairings achieving a S value of > 0.70, except for #79/#54, #15/#132 and #59/#91 (Fig. 5). The ratios and distribution of the time activity patterns indicate a moderate intra-pair synchronization overall ($\bar{S} = 0.75 \pm 0.10$), with an evident overlap in both frequencies, temporal distribution and type of performed activity pattern (see Fig. 3).

Moreover, the simulation of the pairings between each female and all possible male pairings shows that regardless of the mate choice, the synchronicity was always higher with the real partner than with any other male (Exact binomial test, $p < 0.0001$).

A higher synchronicity index was overall associated with a higher likelihood of the pair to lay eggs and producing offspring (Fig. 6), with #135/#71, #140/#193, #82/96, #159/#161, #154/#86 and #116/#124 having sired several chicks before or after the data collection. While the pairing #141/#129 showed an overall high synchronicity index and produced several clutches, none of the eggs proved to be fertile. Poor social behavioral synchronization was associated with low reproductive performance (Fig. 6), as the pairings #79/#54, #15/#132, or #59/#91 did not produced eggs during 2018-(2019)2020 and were consequently separated in 2019 or 2020, respectively.

4. Discussion

Our main objectives for this study were (1) to describe the full suite of non-sexual behaviors of Spix's macaws in captivity, (2) to document their time activity patterns, and (3) to 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 description of a total of 75 non-sexual behaviors, including stereotypies and other behavioral disorders (hereafter, *behavioral disorders*) for the Spix's Macaw (see SM Results & Discussion). Most of these behaviors appear to be similar to those recorded for closely related species in both captive and wild environments (Ulribe 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 already 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, the stereotypical displays we observed are little discussed in the literature, which could imply that some displays are species-specific, or that they are little studied, or both. While no wild parrot has been documented presenting the aforementioned disorders, behaviors we consider as disorders in the context of captivity may occur in nature with a different etiology (see Heinsohn et al. 2011). This is the case of egg destruction and infanticide, which can happen in the wild as a general response to intraspecific or interspecific competition, but which occurred systematically with certain individuals in the focal captive population, while other individuals were never affected.

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,* 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, against 41% for captive conspecifics (Cornejo *et al.* 2005). We recorded Spix's macaws to spend 8.33 ± 1.81 % (5.67-12.38) of their full diurnal activity period foraging, which is lower than what has been reported for *captive* Scarlet macaws (ca. 15 %; 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 according to the environment, foraging activities are reduced in captivity. In their natural environment, parrots spend a substantial amount of time foraging as demonstrated for *released* Scarlet macaws (28%; Cornejo *et al.* 2005), wild Ouvéa Parakeets (*Eunymphicus uvaeensis*) (in average 47%; Robinet *et al.* 2003), or wild Kangaroo Island Glossy black cockatoos (*Calyptorhynchus lathami halmaturinus*) (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 foraging trips ("search flights") to locate feeding sites, the modification of food elements, and eventual interactions with competitors for the access to resources (Chapman & Paton 2005, Brightsmith *et al*. 2018). While comparative data for locomotion are less abundant, we observed Spix's macaws to spend even less time actively moving than foraging, which is also likely to be a response to the captive environment in general (confined space) and to the easy access to food in particular.

By eliminating native constraints (i.e., food limitation, competition, predation), captive conditions induce a shift in activity patterns which may promote the expression of behavioral disorders. Compared to its presumed absence in the wild, we indeed observed the Spix's Macaws to spend on average 3.19% 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 activities (especially lack of social and environmental interactions) combined to stress factors resulting from suboptimal husbandry conditions (e.g., inappropriate hand-rearing, lack of enrichment, poor health management), but other intrinsic factors may also play a role (e.g., personality, stress levels, genetics; see Garner *et al*. 2006, Luescher 2006, Owen & Lane 2006, Cussen & Mench 2015, authors per. obs.).

We believe minimizing the occurrence of behavioral disorders to be an imperative for increasing the success rate of the reintroduction of animals into 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 criterion (inbreeding, relatedness) and to the physical condition of the bird, we thus used the established ethogram to select release candidates based on their behavior – retaining only those showing no evidence of behavioral disorders. Beyond the prospect of release programs, reducing the occurrence of behavioral disorders through the optimization of husbandry protocols is also a way to promote both animal welfare and the productivity of ex-situ populations. This is because such behaviors can lead to physical injuries by auto-mutilation, redirected aggression, feather plucking (Owen & Lane 2006, Luescher 2006, Acharya & Rault 2020). Behavioral disorders in captive parrots can also interfere with breeding readiness and performance. As an extreme illustration, we observed a few females purposefully destroying their eggs during the incubation period or killing their offspring after hatching.

Husbandry should thus 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). In this context, ethological data can serve as an important template to improve husbandry manuals. Several measures were taken to reduce behavioral disorders in ACTP facilities following data collection. For example, the environment of all birds is frequently enriched by providing them with paper rolls, cardboards, new modular toys, treat dispenser toy and fresh greens. We have also progressively favored the rearing of chicks by their parents. We have yet to investigate and disentangle the effects of such changes on the time-activity patterns, but behavioral disorders in ACTP facilities have substantially dropped over time. More will be attempted to continue to bring the 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 so as to induce similar changes could be beneficial.

Behavioral synchronicity and implications for conservation breeding efficiency

Another way to increase the productivity of animals in captivity is to provide individuals with mates 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 choosing their partners as they would do in the wild. Free mate choice has indeed been linked to higher breeding output, including in psittacines (Waugh & Romero 2000, Luescher 2006, Spoon *et al*. 2007), mammals (Martin-Wintle *et al*. 2015, Parrott *et al*. 2019) and reptiles (Lemm & Martin 2023). However, letting animals choose their mates freely is usually not feasible in captivity due to time and space constraints, or due to limited mate availability. Moreover, free mate choice may not always result in the desired outcome from a conservation perspective (e.g., maintaining genetic diversity). Another possibility is to expose, in a controlled setting where no mating is possible, 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 a few species (Martin-Wintle et al. 2015, Alverson et al. 2023), assessing mate preferences in such a way requires a specific layout for the enclosures. The last option is for breeders to adjust pairings based on observed behavior compatibility (Spoon *et al*. 2007, Fox and Milliam 2014).

Breeders tend to consider mates spending 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 higher cohesion and synchrony, and exhibited frequent allopreening and lower aggression (Spoon *et al*. 2007). Raw data of behavior could therefore be helpful to evaluate the intra-pair “harmony” *a priori* and thereby forecast breeding probabilities. These observations suggest that letting individuals express their mate preferences can improve breeding output. However, how to measure such behavioral compatibility when the mate choice is constrained by breeders remains little explored. Our approach was to design a synchronicity metric (*S*) to compare the time activity patterns of each paired individual and to test if such a metric predicted breeding performance.

Our results show that the less synchronous pairs were the lower their fertility rates, suggesting that inadequate mate selection resulted in productivity loss for the breeding program. In the focal facility, pairs with a synchronicity index greater than 0.75 showed good reproductive output, producing a high number of eggs and offspring. Only one pair proved to be the exception (#141/#129). While the pair #141/#129 produced eggs, no offspring resulted from them. A pathological cause seems unlikely, as both #141 and #129 produced offspring with a different partner in 2021 (#141) and 2023 (#129). A poor genetic matching leading to the expression of lethal alleles could be a possible explanation, especially considering that the entire genetic population of the species is based on six founder individuals only (Purchase 2019). The pair #59/#91 did not produced offspring at ACTP, however, sired two offspring in 2017 in Qatar (#216 and #217, Al Awabra, Purchase 2019).

Whenever breeding programs rely on forced pairings, the breeding output could thus be improved by selecting candidate mates using behavioral data (i.e., behavioral profiles, time-activity patterns) in addition to other criterions that may be employed (e.g., age, genetics, previous breeding success). An open question is then, *when to measure synchronicity for yielding best results?* It seems tempting and practical to monitor behaviors and measuring synchronicity in time activity patterns before pairings. However, we observed that in poorly synchronized pairs the majority of females still showed the highest synchronicity with their actual partner in comparison with putative mates. This highlights that synchronicity in time activity patterns is not a static trait, but a variable one 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 with their social flock (see Hobson *et al*. 2014). Even in forced pairings resulting in no sexual activity, the birds thus engage in social tolerance and interaction leading to an increase in synchronicity.

Data are lacking to establish whether or not synchronicity measured before pairing could actually predict breeding output as reliably as synchronicity does when it is measured after pairing. Our experience is that established pairs often shown increased behavioral synchronization within the first six weeks of pairing, which allowed us to assess the pairing success in time before egg laying (VM pers. obs.). Whenever detecting poor synchronicity, we thus either swapped pairs immediately if the synchronicity was really low, or else during the onset of the next breeding season. The proposed approach has been effective in our case as it helped us to reevaluate and adjust >90 % of all pairings between 2018-2024 at ACTP Germany which had either never bred or produced in majority infertile clutches. This resulted not only in a steady increase of offspring numbers (2019 - 11, 2020 – 21, 2021 – 50* up to four clutches were laid by each pair, which we restricted to two for the following years, 2022 – 35, 2023 – 42, 2024 – 44), but also in numbers of parents capable of successfully raising their chicks (2020 – 0, 2021 – 2, 2022 – 3, 2023 – 7, 2024 – 16) and fertility rates (2019 – 39 %, 2020 – 29 % - several young pairs laid, 2021 – 45 %, 2022 – 47 %, 2023 – 47 %, 2024 – 60 %). To attempt increasing the breeding performances even further, we started in 2023 to place groups of six juveniles (3 males and 3 females with low relatedness) together in enriched and enlarged aviaries and let them there until they reached sexual maturity (3 yrs) and freely choose their partner. After this age, which coincides with the appearance of territorial behaviors, each pair will be placed in a separate breeding aviary. Unfortunately, due to the age of the birds, it is too early to know if this alternative mate choice setup results in improved productivity.

5. Conclusions

Our study highlights that monitoring 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 measuring animal welfare objectively and inform the revision of husbandry manuals so as to increase the productivity of ex-situ breeding programs. The discovery of behavioral disorders and of prolonged periods of inactivity among Spix's macaws under human care within the facility of ACTP Germany prompted us to enrich the environment and modify breeding protocols. The finding that behavioral synchronicity among paired individuals is a reliable predictor of breeding performance also prompted us to revise our pairings based on behavioral criteria. We documented here how breeding productivity improved as a result of such changes and a future publication will detail the decrease in the occurrence of behavioral disorders. 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 ensures the greatest chance of reintroduction success. Even after release, ethograms remain useful as they can be used to check if selected birds successfully adjust to their novel environment (as we have done for the two released cohorts of Spix's macaws, 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 practice. We would like to end by urging others to participate in the global effort of integrating descriptive ethology and behavioral ecology within conservation sciences (see also Curio 1996, Bucholz 2007, Snijders et al. 2007, Berger-Tal & Saltz 2016).

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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 with 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
foraging	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
resting	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

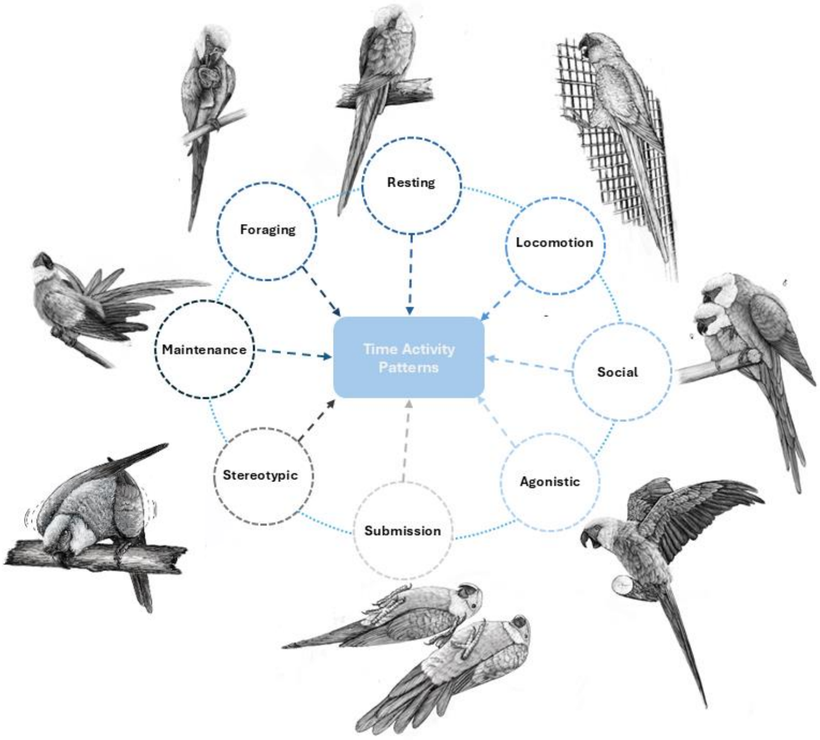


Figure 1 – Behavior categories with characteristic behaviors associated with it and described in the supplementary material, forming the base to define the time activity categories (all illustrations by V. M.). Illustrations for agonistic, submission and stereotypic behavior adapted from Marcuk *et al*. 2020.

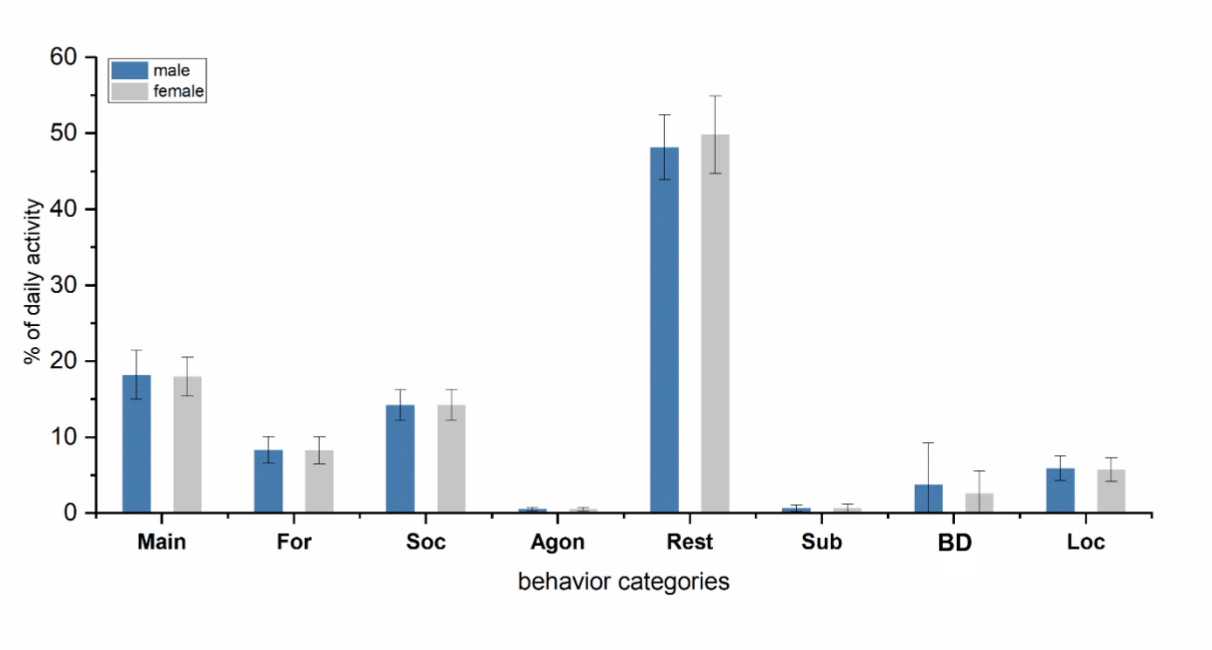
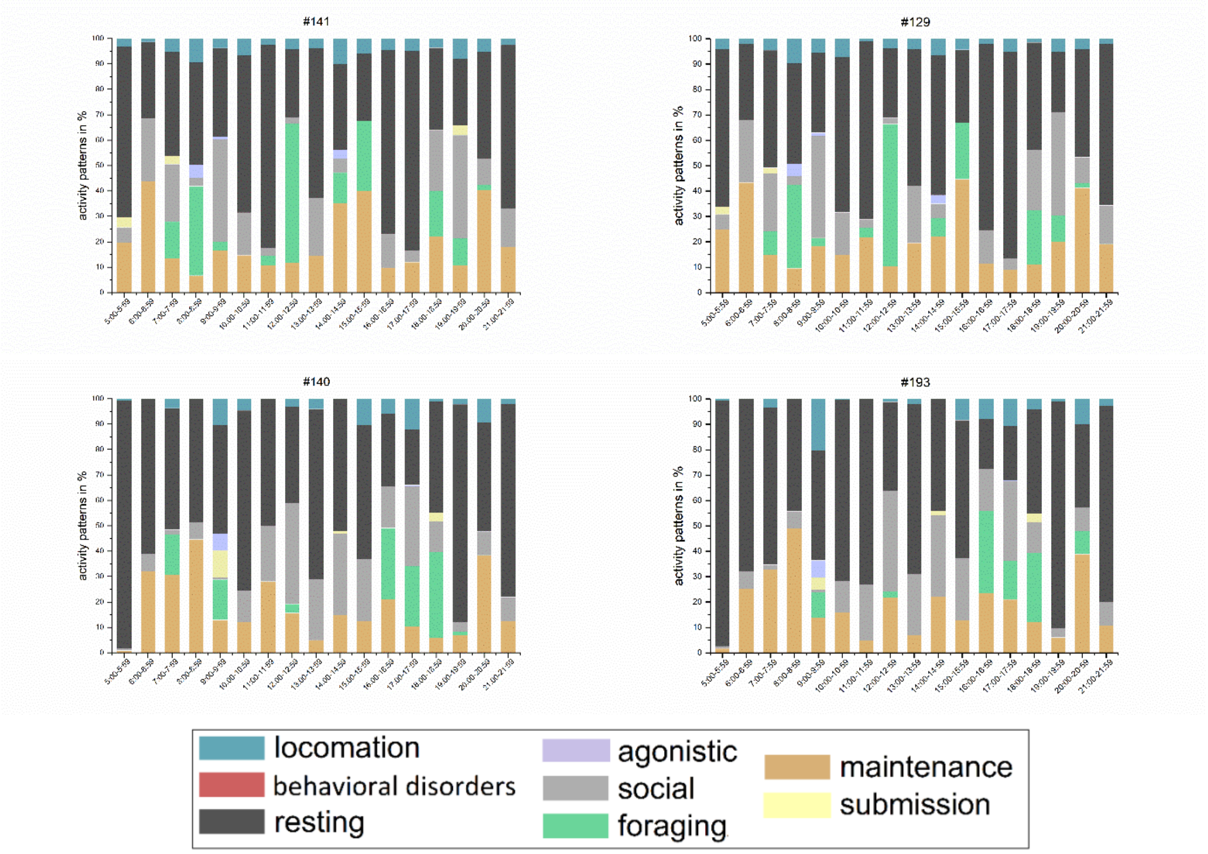
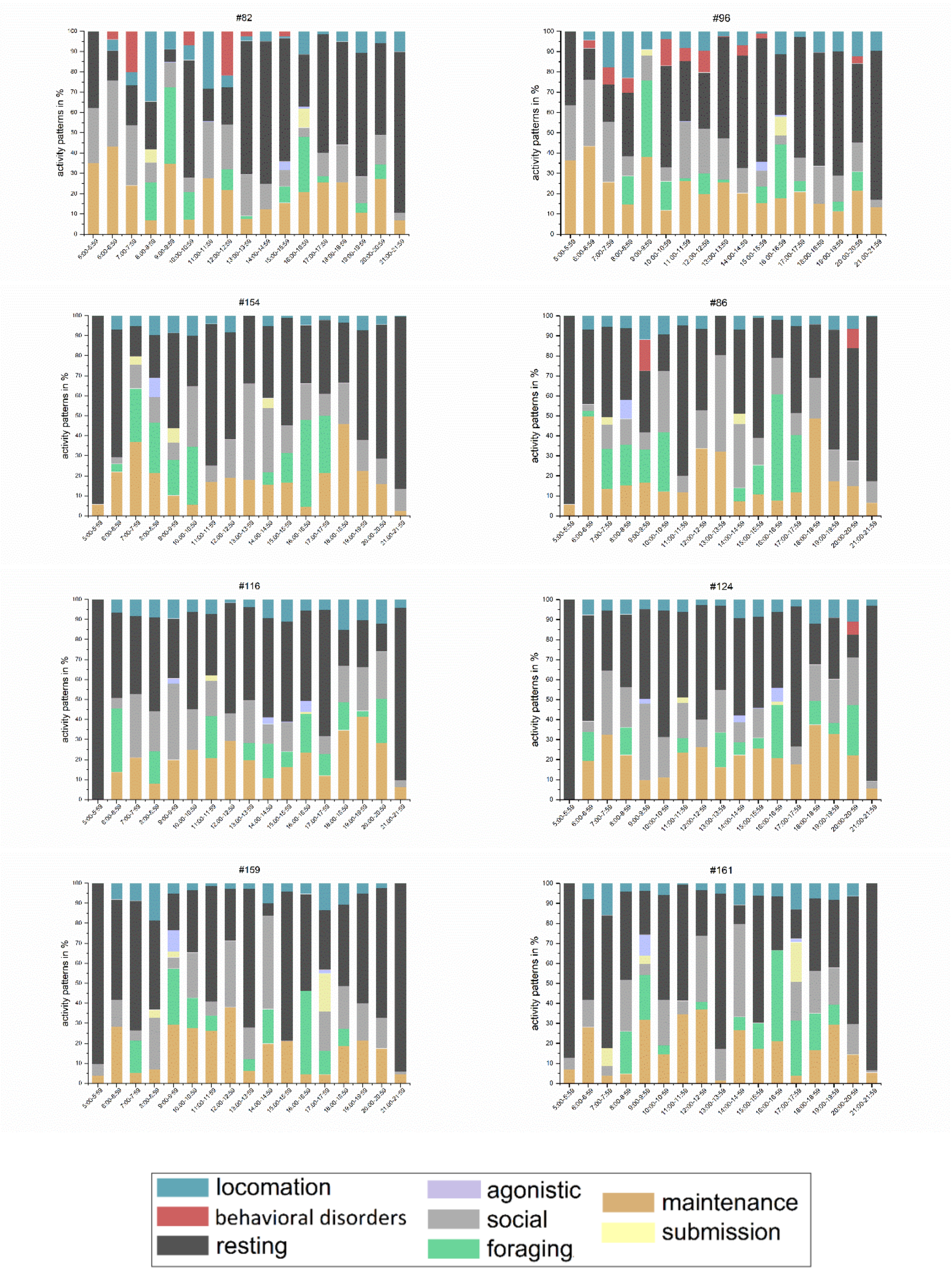


Figure 2 – Time activity budgets of the Spix's macaw under captive conditions, male (blue) and female (orange). **Main** – maintenance; **For** – foraging; **Soc** – social behavior (*identical for both genders); **Rest** – resting; **Loc** – locomotion; **Agon** – antagonistic behavior; **Sub** – submission and **BD** – behavior disorders.


#141
#129
#140
#193
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
locomation
behavioral disorders
resting
agonistic
social
foraging
maintenance
submission


#82
#96
#154
#86
#116
#124
#159
#161
activity patterns in %
0
10
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70
80
90
100
5:00-5:59
6:00-6:59
7:00-7:59
8:00-8:59
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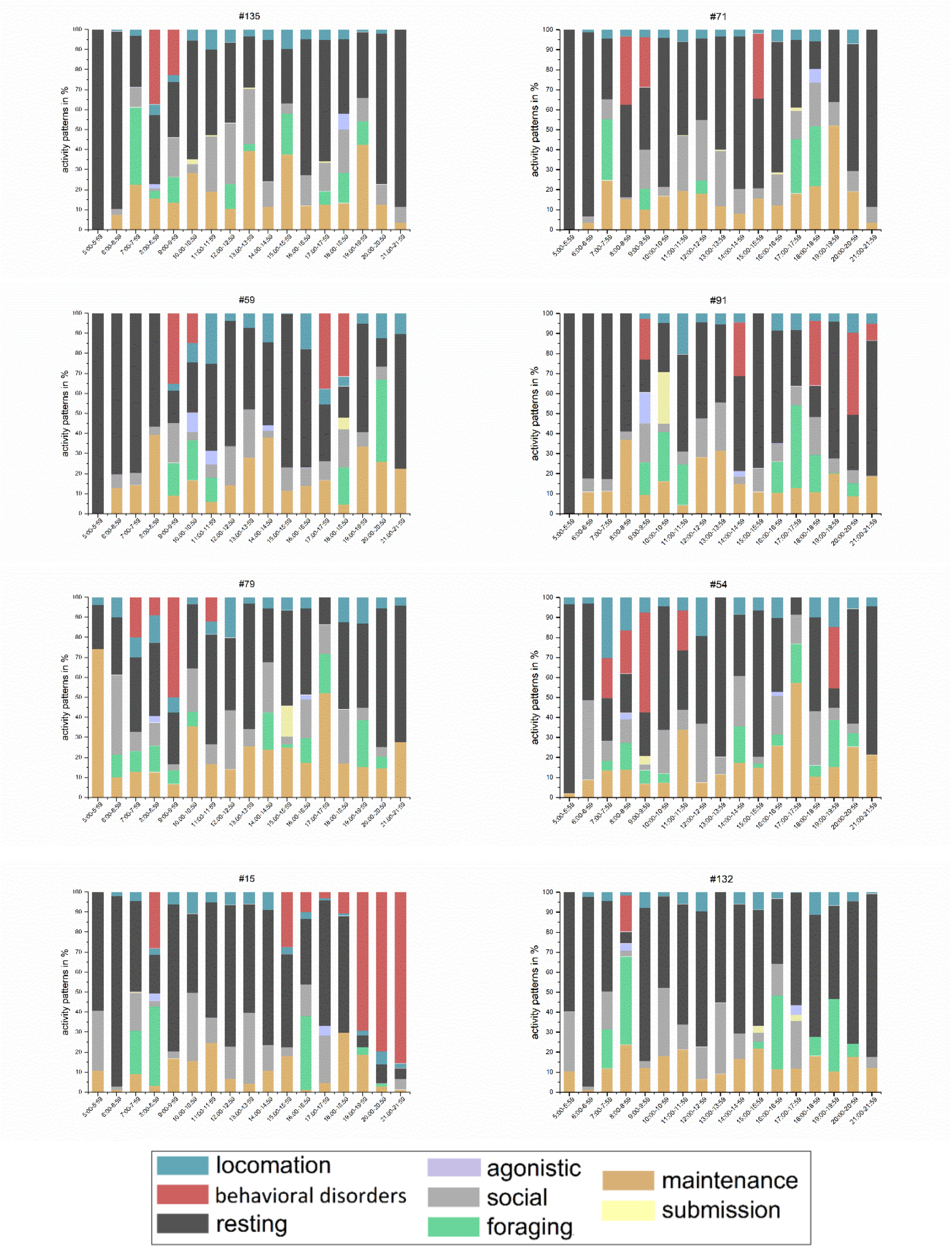

Figure 3 – Diurnal activity patterns of 20 individuals with associated studbook numbers, with each row representing a pair with the male on the left and the female on the right side. Pairs are sorted by decreasing values of intra-pair synchronicity as measured by the metric *S*. Each row represents one pair. Stacked column bars are presented for males on the left and for females of each pair on the right side, respectively.

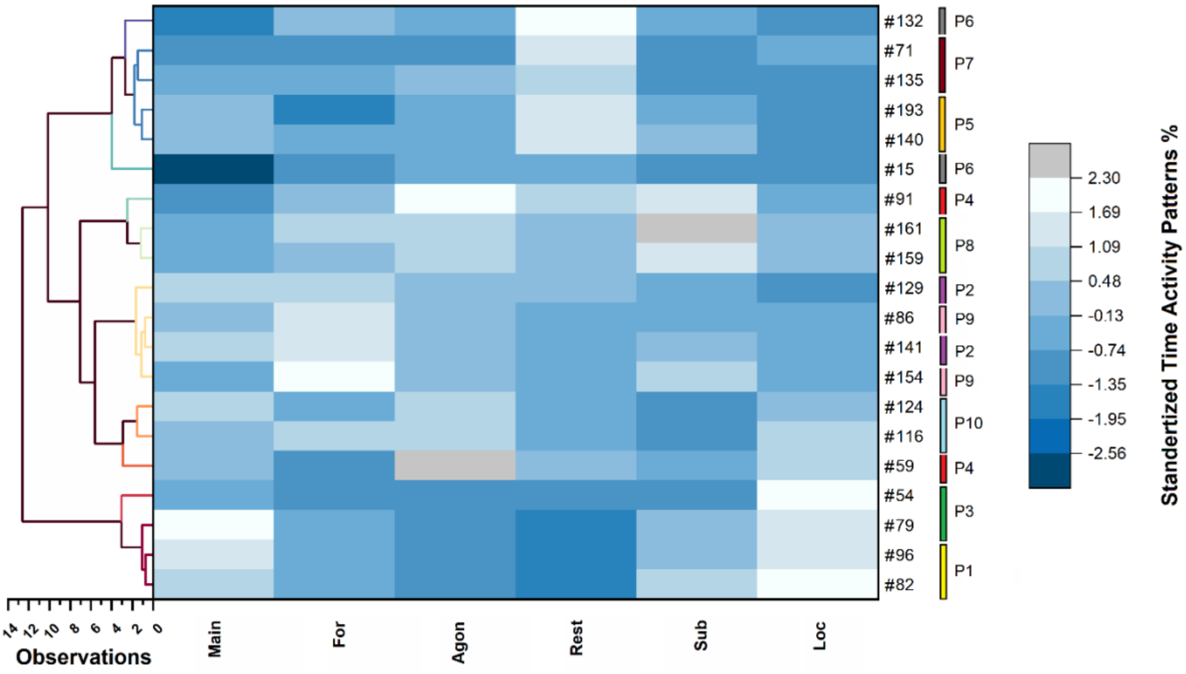

Figure 4 – Heatmap with a hierarchical cluster analysis using standardized data (type = Ward, average type = Euclidean, k = 10 clusters), actual pairs are highlighted (P1-P10) with the associated Studbook numbers, clusters are showing the associated individuals with the highest inter-individual similarity. Social behavior was omitted as it would distort the analysis due to the identical values between female and male.

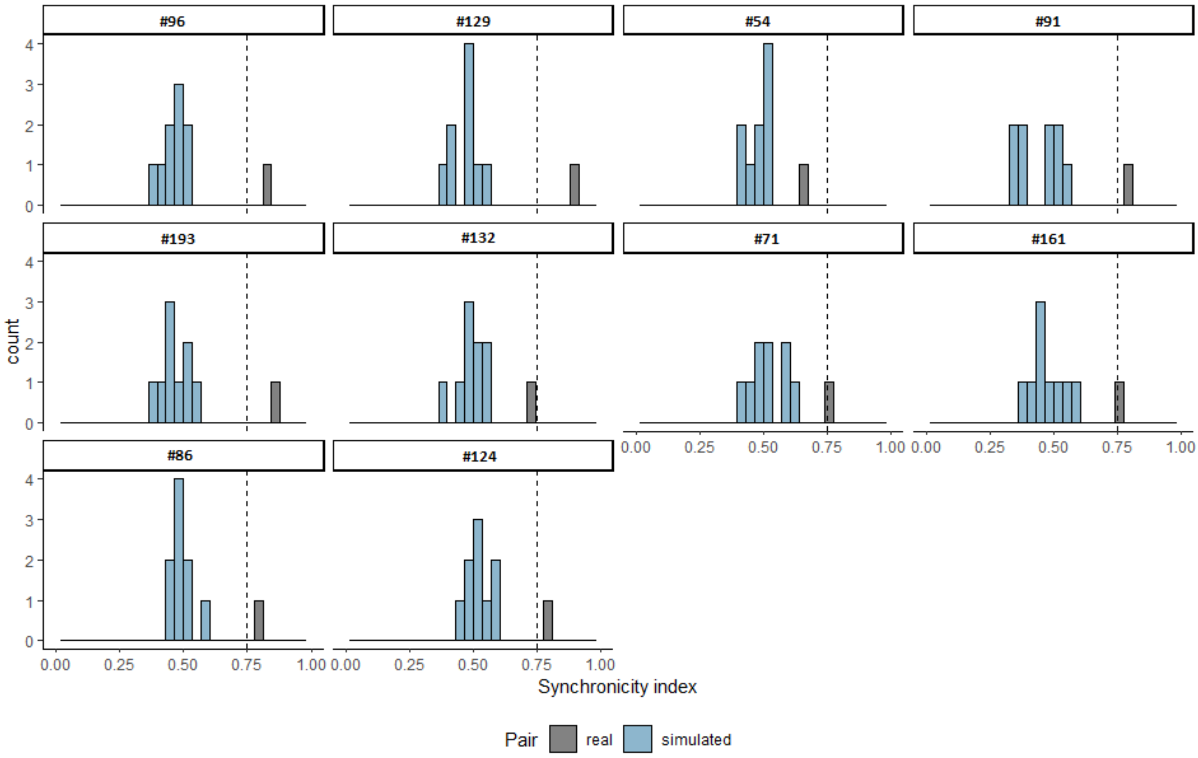

Figure 5 – Synchronicity indices presented for each female, showing the calculated synchronicity index for the actual "real" partner in grey (■) and the simulated partners in blue (■). The studbook numbers of the females are indicated above each plot.

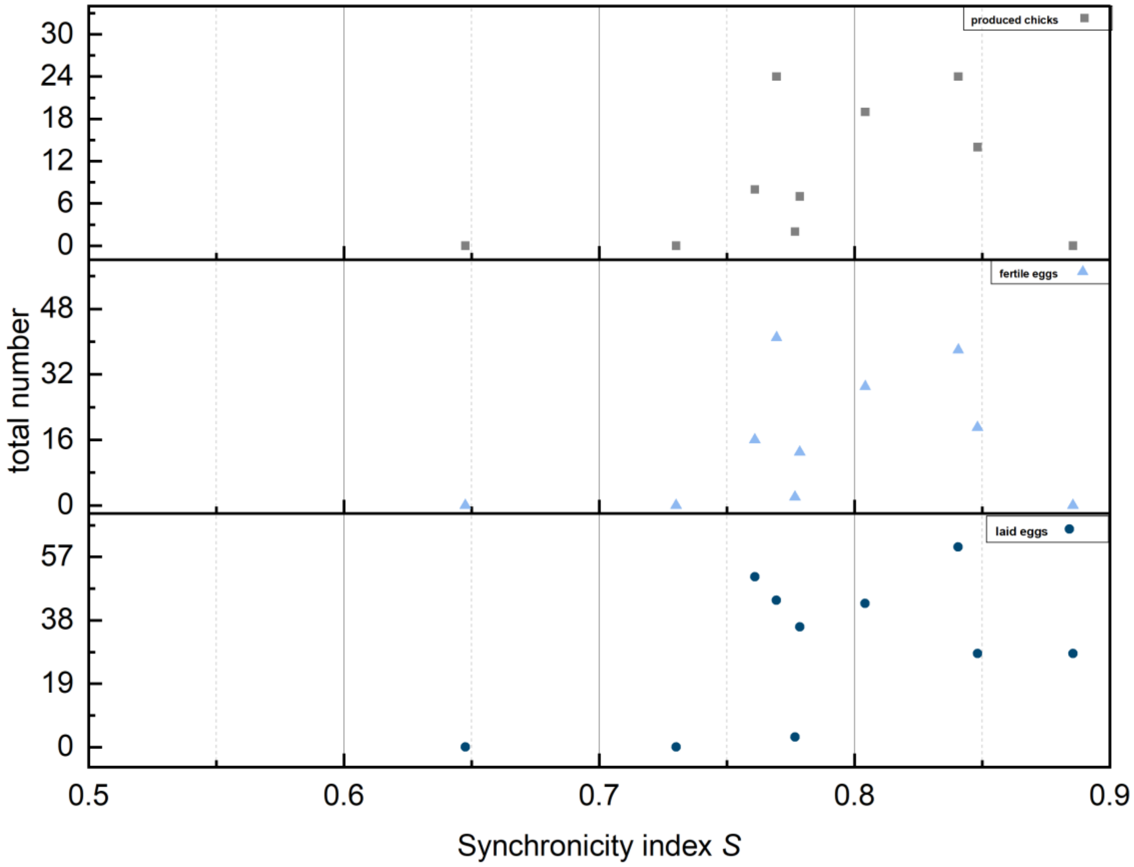

Figure 6 – Scatter plot to illustrate the relationship between Synchronicity index (*S*) of the observed ten pairings and the total number of laid eggs (●), fertile eggs (▲) and chicks (■) produced between 2018-2023.