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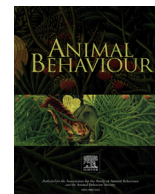


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Looking out for each other: coordination and turn taking in common marmoset vigilance

R. K. Brügger^{*} , E. P. Willems[†] , J. M. Burkart

Department of Anthropology, University of Zurich, Zürich, Switzerland

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For small, arboreal marmoset monkeys, antipredator vigilance is essential to ensure survival. However, since antipredator vigilance is incompatible with some other behaviours, such as feeding in a head-down position, it has to be regulated efficiently within individuals and perhaps even at the group level. To investigate what drives individual differences in vigilance and feeding behaviour in common marmosets, *Callithrix jacchus*, and whether they adjust these behaviours to each other, we collected behavioural data on 14 marmosets in contexts where feeding and vigilance were mutually exclusive. The presence of infants resulted in higher overall vigilance and less feeding. Moreover, individuals increased their vigilance when the pair mate was feeding and thus could not be vigilant itself. They thus adjusted their own vigilance to the risk level of their pair mate, which resulted in a turn taking-like pattern of feeding and being vigilant in the pair. This flexibility of vigilance is consistent with marmosets' sensitivity to other's needs in another context, food sharing, when sharing is increased when food is more difficult to obtain. Together, these results suggest considerable awareness of the current state of group members in common marmosets.

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For many animals the effort to detect threatening stimuli, so called vigilance, is a crucial factor shaping their everyday lives and survival. Vigilance is a main part of most species' behavioural repertoire and is assumed to be costly because it is often performed at the expense of other important activities, in particular foraging (but also resting or social interactions; McNamara & Houston, 1992; Illius & Fitzgibbon, 1994; Bednekoff & Lima, 1998; Unck et al., 2009; Stears et al., 2020; but see Bednekoff & Lima, 2005; Devereux et al., 2006; Cowlshaw et al., 2004; Treves, 2000; Macintosh & Sicotte, 2009; Guillemain et al., 2001). Vigilance is beneficial for individuals as a selfish behaviour, but animals living in a group can also benefit from the 'many eyes effect', i.e. that the sheer number of individuals that are able to be vigilant at a time make predator detection more likely (assuming the information about the detected threat can spread rapidly; Powell, 1974; Lima, 1995).

Such benefits of being in a group can thus emerge when individuals perform their vigilance independently of other group members, and randomly (Pulliam, 1973; Scannell et al., 2001), which avoids the costs of organizing vigilance with others (Bednekoff & Lima, 1998). This does not imply that animals do not

monitor their conspecifics (often referred to as social vigilance [Allan & Hill, 2018; Jack, 2001; Iki & Kutsukake, 2021] in contrast to antipredator vigilance) to gather information about potential competitors, public information (e.g. monitor conspecifics in different food patches), mates or as threats to their offspring (Beauchamp, 2001, 2015), only that they do not take the level of vigilance of others into account when deciding whether to be vigilant themselves or rather engage in a different activity (Beauchamp, 2015). The effects of independent vigilance have been modelled by Pulliam (1973) and empirically supported in multiple species (e.g. ostriches, *Struthio camelus*: Bertram, 1980; house sparrows, *Passer domesticus*: Elcavage & Caraco, 1983; wild boars, *Sus scrofa*: Quenette & Gerard, 1992; degus, *Octodon degus*: Quirici et al., 2008; wombats, *Vombatus ursinus*: Favreau et al., 2009; doves, *Zenaida aurita*: Cezilly & Keddar, 2012). Yet, in several other species the assumption of independent vigilance from Pulliam's model is not met (e.g. greater kudu, *Tragelaphus strepsiceros*: Pays et al., 2012; domestic chicken, *Gallus gallus*: Beauchamp, 2017; common eider, *Somateria mollissima*: Öst & Tieraal, 2011; kangaroo, *Macropus giganteus*: Pays et al., 2009). In these species, vigilance is organized at the group level, and this organization can take two opposite forms: synchronization and coordination.

The synchronization of vigilance by overlapping vigilance bouts with other group members leads to waves of similar levels of

^{*} Corresponding author.

E-mail address: rahelkatharina.bruegger@uzh.ch (R. K. Brügger).

vigilance within a group and might seem a rather counterintuitive strategy of predator avoidance. There are two mechanisms that can explain why the synchronization of vigilance within a group can be beneficial. A vigilant conspecific can be considered as a source of public information about the likelihood of a predator attacking; thus, if many other group members are vigilant an individual may perceive a higher risk of a predator attack and start being vigilant as well (contagion of fear hypothesis; [Beauchamp, 2015](#); [Eilam et al., 2011](#); [Siro, 2006](#)). By becoming vigilant themselves, individuals can verify the social information with individual information about the predation risk and adjust their antipredator behaviour accordingly. These contagion effects that lead to synchrony are thus most likely when others have already detected a threat, perhaps signalling with warning vocalizations, compared to quiet situations when vigilant individuals are calmly checking the environment without being aroused.

Another mechanism that can explain why synchronizing vigilance in a group can be beneficial takes the predator targeting behaviour into account (predator targeting behaviour hypothesis; [Beauchamp, 2015](#); [Siro & Touzalin, 2009](#)). If a predator is more likely to attack individuals that are lagging behind when escaping, it is advantageous to be vigilant if conspecifics around are vigilant as well, to lessen the chances of being the laggard. Vigilance synchronization has readily been shown in several different species of mammals and birds, often by comparing the observed proportion of time at least one group member is vigilant to the predicted proportion of time under the assumption of group members scanning their environment independently. If group members synchronize their vigilance bouts the observed time at least one individual is vigilant is expected to be lower than predicted under the assumption of independent scanning (e.g. birds: [Beauchamp, 2009](#); [Favreau et al., 2009](#); [Fernández et al., 2003](#); [Ge et al., 2011](#); [Öst & Tierała, 2011](#); marsupials: [Pays et al., 2009](#); [Pays, Jarman, et al., 2007](#); ungulates: [Michelena & Deneubourg, 2011](#); [Pays et al., 2012](#); [Pays, Renaud, et al., 2007](#)).

Coordination of vigilance occurs when animals minimize overlapping vigilance bouts and thus maximize the time when at least one group member is vigilant. This leads to collective benefits for predator detection ([Rodríguez-Gironés & Vásquez, 2002](#)). Successful coordination requires that individuals perceive whether others are vigilant as well as adequate information transfer ([Fernández-Juricic et al., 2004](#)). Sentinel behaviour is a typical ([Beauchamp, 2015](#)) yet rare ([Bednekoff, 2015](#)) form of vigilance coordination. Sentinelling individuals are vigilant for the whole group, often from an elevated position, without foraging ([Bednekoff, 2015](#)). Sentinel systems have predominately been found in cooperatively breeding species such as meerkats, *Suricata suricatta* ([Clutton-Brock, 1999](#); [Manser, 1999](#); [Rasa, 1986](#)), or cooperatively breeding birds (Arabian babblers, *Argya squamiceps*: [Wright, Berg, et al., 2001](#); [Wright, Maklakov, et al., 2001](#); [Ostreiher et al., 2021](#); scrub jays, *Aphelocoma californica*: [McGowan & Woolfenden, 1989](#)), likely due to inclusive fitness benefits ([Ridley et al., 2013](#); [Santema & Clutton-Brock, 2013](#); [Bednekoff, 2015](#)); but see [Clutton-Brock, 1999](#); [Wright, Berg, et al., 2001](#)). Even though there are numerous anecdotes and descriptive accounts of sentinel behaviour, its defining feature, namely that animals coordinate their vigilance bouts (compared to synchronized vigilance coordinated vigilance would imply that group members maximize the time at least one individual is vigilant; [Beauchamp, 2015](#)), has rarely been tested ([Bednekoff, 2015](#)). In addition, empirical evidence for coordination outside of species in which a sentinel system is documented is even harder to find and has mostly been reported for pairs of individuals, namely in coral reef fish ([Brandl & Bellwood, 2015](#); [Fox & Donelson, 2014](#)), mating pairs of white-tailed ptarmigans, *Lagopus leucura* ([Artiss et al., 1999](#)) and pairs of

common cranes, *Grus grus*, in an area with high likelihood of human disturbance ([Ge et al., 2011](#)). Importantly, once a sentinel detects a threat, this is signalled to other group members which then will also become vigilant, leading to synchronized vigilance. Patterns of both coordination and synchronization of vigilance within in the same species are thus not contradictory but can be the result of situation-specific factors.

For both synchronization and coordination, the vigilance level of conspecifics needs to be taken into account. This can be achieved in cognitively undemanding ways, such as behavioural contagion ([Eilam et al., 2011](#), resulting in synchronization), or via simple behavioural rules (e.g. stop being vigilant when a sentinel is signalling he is on duty [[Wickler, 1985](#); [Manser, 1999](#); [Kern & Radford, 2013](#)], resulting in coordination). However, vigilance can be organized in a much more flexible way if individuals additionally take others' specific behaviours and the associated risk levels into account. For instance, field experiments with chimpanzees, *Pan troglodytes*, which have special alarm calls ('alert hoot') to warn conspecifics about low-level threats, have shown that they are able to take into account whether a conspecific had already seen a threat or not, and were particularly likely to signal in the latter case ([Crockford et al., 2012, 2017](#)). Likewise, captive adult squirrel monkeys, *Saimiri boliviensis* ([Biben et al., 1989](#)) and golden lion tamarins, *Leontopithecus rosalia* (reintroduced and wild individuals; [de Oliveira et al., 2003](#)) were especially vigilant when immatures were at play, and the tamarins did so with their backs turned towards the playing immatures, being vigilant towards the outside. In such instances, vigilance and warning behaviours cannot serve a selfish function only but are part of a cooperative act, and they appear to reflect some understanding of the group members' risk, and perhaps even that their risk is different from their own.

Here we investigated the flexibility of antipredator vigilance behaviour in captive pairs of common marmosets, *Callithrix jacchus*. They belong to the family of the cooperatively breeding callitrichid monkeys, small (< 700 g) arboreal primates vulnerable to many predators in the wild ([Ferrari, 2009](#); e.g. raptors: [Izawa, 1978](#); [Vasquez & Heymann, 2001](#); carnivores: [Goldizen, 1987](#); [Stafford & Ferreira, 1995](#); snakes: [Heymann, 1987](#); [Corrêa & Coutinho, 1997](#); [Teixeira et al., 2016](#)). In captivity, they maintain high levels of vigilance and, for instance, react to unfamiliar humans with antipredator behaviour, or keep giving warning calls to the sight of birds of prey through glass roofs or in outdoor enclosures (R.K. Brügger & J.M. Burkart, personal observation). We expected some degree of flexibility in their vigilance behaviour for several reasons. First, marmoset and callitrichid vigilance has been investigated previously (e.g. [Barros et al., 2004](#); [Caine, 1998](#); [Caine & Marra, 1988](#); [Koenig, 1994, 1998](#); [Nunes et al., 2010](#)), and some studies hint at the possibility of a sentinel system in common marmosets ([Koenig, 1994, 1998](#)). Others have found a sex effect, with the highly prosocial males ([Burkart et al., 2007](#)) being more vigilant than females ([Koenig, 1998](#); [Savage et al., 1996](#)), as well as a general negative group size effect on antipredator vigilance ([Gosselin-Ildari & Koenig, 2012](#)). The social system of callitrichids relies heavily on cooperation and they exhibit high levels of allomaternal care ([Burkart et al., 2014](#); [Burkart & van Schaik, 2020](#)), which makes them likely candidates for nonselfish vigilance behaviour that is sensitive to others' risk. Moreover, in food-sharing situations, they appear to take the need of others into account (lion tamarins, *Leontopithecus chrysomelas*: [Moura et al., 2010](#); cottontop tamarins, *Saguinus oedipus*: [Humble & Snowdon, 2008](#); marmosets: [Martins & Burkart, 2013](#)). Finally, marmosets have been found to coordinate their behaviour skilfully in different contexts, such as vocal communication (turn taking, [Takahashi et al., 2013, 2016](#)) and their motor actions in a joint action task ([Miss & Burkart, 2018](#)).

In animals that lower the head for foraging, as for instance in grazing animals, vigilance is typically incompatible with foraging (but see evidence from birds, where head down foraging is not fully incompatible with feeding, [Fernández-Jurícic, 2012](#); [Fernández-Jurícic et al., 2004](#); [Lima & Bednekoff, 1999](#)), and the feeding context is therefore particularly suitable to assess coordination or synchronization of vigilance (e.g. [Brandl & Bellwood, 2015](#); [Ge et al., 2011](#); [Pays et al., 2012](#); [Pays, Renaud, et al., 2007](#)). However, for upright feeding primates (i.e. species that have a diet consisting of mainly fruits, insects and/or leaves) it is less likely that feeding will fully impede the ability to be vigilant ([Treves, 2000](#)). In our study, we avoided this shortcoming by taking advantage of a feeding situation where marmosets are unable to simultaneously feed and be vigilant, namely when eating their mash in the morning from opaque feeding bowls. We thus used this daily feeding situation where animals are unable to feed unless they place their head in the food bowl to lick up the provided mash. This mandatory feeding position would therefore not allow them to simultaneously be vigilant since their eyes are covered by the food bowl during eating. In this situation, we had repeatedly observed how individuals would apparently take turns in putting their heads into the bowl, which may correspond to true coordination of vigilance. Alternatively, it may simply be an artefact of having a single food bowl, from which two animals are able to feed together but are rather unlikely to do so due to lack of space to feed comfortably. We therefore implemented a two-by-two design that controlled for the space restrictions of only one food bowl, by providing either one or two food bowls. We also varied the location of the feeding bowls between the regular indoor home enclosure and the outdoor enclosures, which provided a known environment but slightly higher risk situation because of higher visibility and the likelihood of threatening stimuli (cats walking by or birds of prey flying over the enclosures), and it was new for the marmosets to receive their mash there.

The goal of this study was threefold. In part 1, we investigated determinants of individual variation in vigilance and feeding, predicting higher vigilance in males than females, in pairs with young infants, and outside more than inside. However, we overall expected no difference in vigilance when one or two feeding bowls were available. If vigilance and feeding were regulated only within the individual, we would expect a trade-off between these two activities, especially outside where perceived threat is arguably higher. If, in addition, social factors were taken into account, this trade-off may have been weaker or even absent, because the decision to be vigilant or not may also be influenced by the behaviour and situation of the partner.

In part 2 of the study, we investigated how vigilance was organized overall at the pair level. We therefore compared the observed percentage of time when at least one group member was vigilant to the percentage that would be predicted under the assumption of independent scanning. Since the synchronization of vigilance has advantages in regulating individual antipredator responses (i.e. verifying whether there is indeed a threat), and since marmosets are sensitive to the behaviour of group members in a variety of contexts ([Bugnyar & Huber, 1997](#); [Burkart & van Schaik, 2009](#); [Miss & Burkart, 2018](#); [Voelkl & Huber, 2000, 2007](#)) it can be expected that they would synchronize with others and respond to vigilant group members by becoming vigilant themselves. On the other hand, our observations focused on quiet periods when no external events that may have triggered vigilance were present and when synchronized vigilance is thus less likely. The focus on these quiet periods was chosen to be better able to capture potential coordination of vigilance behaviour.

In part 3 of the study, we investigated whether marmosets would also coordinate their vigilance, and in particular adjust their

own level of vigilance, to the degree of exposure to threat or risk level of the partner. If an individual with its head inside the food bowl was indeed perceived as particularly vulnerable and at risk, we expected that partners would show higher levels of vigilance when their mate's head was inside the feeding bowl than when not. In addition, we also analysed whether animals sitting on the basket that served as the feeding platform containing the bowls would indeed take turns in having their head inside the bowl. This analysis was done in two steps. First, we investigated whether pair mates would overall minimize the time when both had their head inside the bowl(s) simultaneously and compared the observed time of simultaneous feeding to what is expected when both were feeding independently (analogous to the analysis for how vigilance was organized overall at the pair level, described above for part 2 of the study). Second, we analysed the latencies to a behavioural change from either pair mate when animals were performing opposite behaviours (one individual feeding and one individual vigilant, subsequently called opposite states) compared to when both individuals would feed or be vigilant simultaneously (matched states). If animals indeed take turns in feeding and avoid being in the same state, the latencies to change behaviour should be longer in opposite than matched states. Importantly, for all analyses in part 3 of the study (namely, higher levels of vigilance when the partner was feeding, minimizing the time when both would have their head inside the bowl as well as longer durations of opposite intervals) positive evidence would suggest coordination only if it occurred not merely in the one-bowl situation but also in the two-bowl situation. Given the overall high attentiveness to group members, and our spontaneous observations of turn taking when on the basket, we expected that the marmosets would coordinate their vigilance and take the behaviour and risk level of their mates into account when doing so.

METHODS

Subjects and Housing

We collected data on 12 pair-housed individuals (five breeding pairs and one pair of siblings) and one family group with their first 1–4-week-old infant twins (14 adults in total, see [Appendix Table A1](#) for detailed information on all subjects and testing order). All animals were housed in heated indoor enclosures (2 × 1 m and 2 m high) with access to outdoor enclosures (2.4 × 3.2 m and 1.8 m high; under appropriate weather conditions, i.e. temperature > 10 °C). Enclosures were equipped with ample climbing and enrichment structures, including wooden beams, natural branches, ropes, heated resting platforms and sleeping boxes. The floor was covered with bark mulch. Monkeys were fed at least twice a day: in the mornings with a vitamin-enriched mash and at midday with fresh fruit and vegetables. In the afternoons they received additional snack feedings with various protein sources (eggs, nuts, insects). Water was always available *ad libitum*.

Procedure, Data Coding and Preparation

All experiments were carried out in accordance with the Swiss legislation and licensed by the Kantonales Veterinäramt Zürich (licence number: ZH223/16; degree of severity: 0).

Procedure

Data were collected during regular morning feedings between 0815 and 0900 hours (except for one session starting at 0730). To be able to control for environmental factors influencing vigilance levels, we implemented a 2 by 2 design varying the location of the morning feeding and the number of food bowls in which animals

received their mash (keeping the amount of food provided constant). Locations differed between 'inside' (designating the inside part of the home enclosures), where animals are used to being fed and normally get all their meals, and 'outside' (designating the outdoor part of the home enclosures, accessible via a semi-transparent tube system), where animals are used to spending time but normally do not receive any food, especially not the morning mash. The animals fed from either one or two bowls, so that we could account for potential space effects. Even though it is possible for two animals to feed simultaneously from the same bowl, it requires them to have their heads very close together which could influence coordination of feeding or vigilance if they want to avoid feeding in such close proximity. All animals experienced the four conditions in a semirandomized order (we split up half of the groups to experience either location 'inside'/'outside' first as well as either number of bowls first; see [Appendix Table A1](#)), resulting in a total of 28 sessions. The sessions were filmed over the course of 5 weeks in May 2018 with one to three sessions per week but only ever one session per group per day.

During the feeding the experimenter was not present, to exclude effects of vigilance towards the experimenter. The experimenter placed the food bowls in a feeding basket at the front grid of the home enclosure before starting the session immediately after leaving the home enclosure (location 'inside') or granting animals access to the outdoor enclosures (location 'outside').

All animals were filmed with one or two video cameras (Sony HDR-CX730/HDR-CX200) placed inside or outside their home enclosures to provide a general overview of the whole enclosure as well as a more detailed recording of the feeding basket. Cameras were left running for 15–30 min, to ensure the whole feeding session was captured for each group (different groups were known to feed faster or slower), but we only coded specific sections of the videos according to predefined criteria (see Data coding and preparation below).

Data coding and preparation

Behavioural coding. Behaviours were coded continuously for all adult individuals with the software INTERACT (Mangold GmbH, version 18.0.1.10, Arnstorf, Germany). The behavioural coding started with the first frame when the experimenter was no longer visible (location 'inside') or the first individual was located with all four limbs outside of the connecting tube to the outside enclosure (location 'outside'). We excluded any time periods during the session when animals did not feed for longer than 4 min. Sessions were considered finished either when animals stopped eating because all the mash provided was eaten, they stopped eating for more than 4 min without resuming eating or after 10 min (for a detailed overview of the length of sessions see [Appendix Table A2](#)) resulting in a total duration of 210 min 13 s. Additionally, we excluded periods with obvious outside disturbances that would induce vigilance (we were interested in the effects on pre-emptive vigilance not reactionary vigilance, see [Boinski et al., 2003](#)), for example, a cat walking past the front of the outside enclosure, or other groups vocalizing loudly. Specifically, we coded vigilance, out of sight and feeding behaviour as well as the locations of the animals according to the definitions in [Table 1](#).

We tested for interobserver reliability. We reached an interclass correlation coefficient (ICC 3) of 0.95 (95% confidence interval, CI [0.86, 0.98]) for vigilance, 1 (95% CI [0.99, 1.00]) for feeding and 0.94 (95% CI [0.85, 0.98]) for the location categories by coding 21% of all video data by a second rater.

Data preparation and calculation of variables. After coding, we exported raw coding files with the start and end time for each behaviour and location of the individuals, and subsequently

Table 1

Ethogram with definitions for all behaviours and locations coded from video material

| | Definition |
|------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Behaviour | |
| Vigilance | All looking behaviour (≥ 1 s) directed over arm's reach and not towards a group member or the substrate the animal is sitting on (following Allan & Hill, 2018) |
| Out of sight | All looking behaviour (≥ 1 s) where the line of sight is not clearly discernible, but the animal could potentially be vigilant |
| Feeding | Since the mash can only be eaten when licking it out of the food bowl, the feeding starts with the first frame of the subject's head inside the bowl, meaning the upper corner of the white ear tufts is no longer visible and it ends with the first frame of the edge of the ear tufts becoming visible at the upper edge of the bowl |
| Location | |
| Inside/outside | Location 'inside': all animals can a priori only be inside, not outside. Location 'outside': animals access the outdoor enclosure via a tube from the inside enclosure. They have access to part of the tube where they cannot see the outside enclosure and are thus considered 'inside' until the first frame in which all limbs are fully outside the tube and as soon as one limb is inside the tube, and 'outside' in all other situations |
| On basket | Animals are considered to be on the feeding basket at the front of the enclosure (inside/outside) starting with the first frame in which one limb is on the feeding basket until the last frame in which a limb is visible on the feeding basket |

processed the data with custom python scripts (version 2.7; <https://www.python.org/>) that allowed us to export the necessary variables for statistical analysis.

Variables for part 1. We calculated the proportion of time an individual was vigilant as the percentage of total time observed of the specific session (adjusted for the time the focal individual was out of sight, by subtracting the time an animal was out of sight from the total observation time) an individual was being vigilant ($P_{A\text{vig}}$ or $P_{B\text{vig}}$, A and B stand for either individual of the group). Similarly, we calculated feeding proportion as a percentage of the total time an individual was feeding ($P_{A\text{feed}}$ or $P_{B\text{feed}}$).

Variables for part 2. We calculated the probability of at least one individual being vigilant under the assumption of independent scanning (predicted group vigilance) and the observed probability of at least one individual being vigilant (observed group vigilance) per session and restricted to the time when both individuals were in sight. Predicted group vigilance assuming both individuals are scanning independently is given by $1 - [(1 - P_{A\text{vig}}) \times (1 - P_{B\text{vig}})]$, where $P_{A\text{vig}}$ and $P_{B\text{vig}}$ designate the respective proportions of time either adult individual of the group is vigilant (and were identical to the values used for part 1; e.g. [Ge et al., 2011](#); [Pays, Renaud, et al., 2007](#)). Observed group vigilance was calculated by dividing all instances where at least one of the individuals was vigilant over the total time of the session controlled for out of sight. If observed group vigilance is lower than predicted (more overlapping vigilance bouts than would be expected if individuals scan independently) individuals synchronize their vigilance; if the opposite is the case (fewer overlapping vigilance bouts than expected under the assumption of independent scanning), individuals coordinate their vigilance ([Beauchamp, 2015](#); [Ge et al., 2011](#)).

Variables for part 3. The two conditional probabilities (an individual's vigilance during a feeding bout of their pair mate and the individual's vigilance at any other time, i.e. during all nonfeeding

periods of their group mate) were expressed as proportions of time: $P_{\text{A}|\text{B}}^{\text{A}|\text{B}} = \text{Time}_{\text{A}|\text{B}}^{\text{A}|\text{B}} / \text{Time}_{\text{B}}^{\text{B}}$ and $P_{\text{A}|\text{B}}^{\text{A}|\text{B}} = \text{Time}_{\text{A}|\text{B}}^{\text{A}|\text{B}} / \text{Time}_{\text{B}}^{\text{B}}$.

In a separate analysis, we used only times when both individuals were located on the feeding basket. Similar to our analysis in part 2, we calculated the predicted probability of simultaneous feeding of both individuals under the assumption that feeding bouts happen independently as: $P_{\text{A}|\text{B}}^{\text{A}|\text{B}} = P_{\text{A}|\text{B}}^{\text{A}|\text{B}} \times P_{\text{B}|\text{A}}^{\text{B}|\text{A}}$, whereas $P_{\text{A}|\text{B}}^{\text{A}|\text{B}}$ and $P_{\text{B}|\text{A}}^{\text{B}|\text{A}}$ are the observed probabilities of feeding bouts when both individuals are together on the basket (so near the food bowl) calculated per session. Lastly, the observed probability of both individuals feeding simultaneously (and thus both being situated on the feeding basket) is given by: $P_{\text{A}|\text{B}}^{\text{A}|\text{B}} = \text{Time}_{\text{A}|\text{B}}^{\text{A}|\text{B}} / \text{Time}_{\text{A}|\text{B}}^{\text{A}|\text{B}}$. If the observed probability of simultaneous feeding is lower than the predicted value, individuals take turns feeding and minimize the time they are feeding simultaneously; if the opposite is true, individuals are more likely to feed synchronously.

For the same restricted time when both animals were situated on the feeding basket, we further calculated latencies until the next behavioural change (either from feeding to being vigilant or vice versa) of either animal from each start of a new behaviour. Thus, the first animal to change its behaviour as soon as both animals were sitting on the feeding basket was considered the reference animal until the next behavioural change happened. At that timepoint the animal that changed its behaviour was considered the reference. If no behavioural change from the nonreference animal occurred until the reference animal was changing the behaviour again, this interval was considered censored. The intervals were then assigned an interval 'type' depending on the behaviours both individuals were exhibiting during the current interval. If both individuals were feeding or both were vigilant the interval was considered 'co-feeding' or 'co-vigilant'; if one individual was feeding and the other one vigilant the type was set to 'opposite'. If animals changed their behaviours simultaneously the previous interval was discarded, and a new interval only started with the next behavioural change. Since animals could both interrupt their behaviours for multiple seconds (to swallow, check how much food is left in the bowl, glance at partner) these interruptions or breaks in between the clear start of a new behaviour or continuation of the old behaviour would only be considered a true interruption when lasting longer than 3 s (only around 20% of all interruptions were over 3 s) and subsequently set to 'other'. Intervals that contained either behaviour 'feeding' or 'vigilant' and 'other' were discarded (386 intervals included for analysis; 145 intervals discarded). If animals indeed take turns, intervals with opposite behaviours are predicted to be longest.

Statistical Analysis

All statistical analyses were conducted in R (version 3.5.3; R Core Team, 2015). We used a Bayesian linear mixed modelling framework as implemented in the 'brms' and 'rstan' packages (Bürkner, 2018, 2017; Stan Development Team, 2020). Since our two outcome variables for models 1–4 represent proportions (i.e. the per trial ratio of the time an animal was vigilant/or feeding over its total observation time, accounting for the time the animal was out of sight), we opted to fit models based on the family of (zero-inflated) beta distributions. In model 5 the outcome variable was time-to-event data, and we thus fitted a Cox proportional hazards model (family 'cox'). Model performance was assessed by graphical posterior predictive checks, and by calculating a Bayesian version of the R^2 statistic (Gelman et al., 2019). For each model we provide several measures to draw inferences (McElreath, 2016; McShane

et al., 2019): we report parameter estimates for fixed effects, along with their standard error, nested 69, 89 and 97% credible intervals (to communicate the shape of the posterior distribution, McElreath, 2016), as well as the proportion of the posterior distribution smaller (p_-) or larger (p_+) than 0. In contrast to frequentist P values, these values quantify the total support generated by the model for a negative or positive effect, given the data at hand (Martin et al., 2021). For further specifications of the modelling process see the Appendix.

Individual variation in vigilance and feeding

Our first analysis modelled the proportion of time per experimental session that each individual in a group was either vigilant or feeding as the two (related) outcomes in a multivariate generalized linear mixed model (GLMM; model 1). We included the presence of infants in the group (yes, no), the sex of the focal individual (male, female), the number of bowls provided during the experimental session (1, 2) and the location of the experiment (inside, outside) as fixed effects for both proportions. Group and individual were added as (nested) random intercepts to control for the dependency structure of the data. The extent of potential covariance between the two outcome variables was assessed at the between-individual level (within each group) to establish whether there was indeed a trade-off between them.

Group vigilance

To understand how group vigilance was regulated and whether individuals' vigilance within a group was synchronized, we calculated the probability of at least one individual being vigilant under the assumption of independent scanning (predicted group vigilance) and compared this value to the observed probability of at least one individual being vigilant (observed group vigilance). A beta GLMM (model 2) was fitted with group identity as a random intercept, and we were interested in the effect of 'type of group vigilance' (predicted, observed), controlling for the potentially confounding effects of presence of infants in the group (yes, no), the number of bowls (1, 2) and location (inside, outside) as fixed effects.

Coordination and turn taking of vigilance and feeding

To analyse whether individuals were able to change their vigilance behaviours in response to the risk level of group members, we compared the conditional probabilities of an individual's vigilance during a feeding bout of their fellow pair mate with the individual's vigilance at any other time (i.e. during all nonfeeding periods of their pair mate). We fitted a beta GLMM (model 3) with individual and group as (nested) random intercepts and were interested in the effect of context (vigilance during feeding, vigilance during non-feeding), controlling for the potentially confounding effects of the presence of infants in the group (yes, no), the number of bowls (1, 2) and location (inside, outside).

Next, we investigated the degree of turn taking and coordination of the feeding and vigilance bouts when both animals were sitting on the feeding basket. To do so we compared the predicted probability to the observed probability of both individuals feeding simultaneously to test whether they would minimize simultaneous feeding. We fitted a (Bayesian) beta GLMM (model 4) with group and individual as (nested) random intercepts and were interested in the effect of 'type of simultaneous feeding' (predicted versus observed simultaneous feeding), controlling for the presence of infants in the group (yes, no), the number of bowls (1, 2) and location (inside, outside).

Finally, we compared the time to the next behavioural change (dependent variable model 5) of co-occurring behaviours with a (Bayesian) cox proportional hazards GLMM. We investigated the effects of type of interval (opposite [either individual is feeding or

vigilant], co-feeding, co-vigilance), while controlling for the effects of the reference individual (male, female), number of bowls (1, 2), location (inside, outside) and whether the reference individual's behaviour was interrupted (yes, no). To control for repeated measures within individuals and multiple bouts of individuals being on the feeding basket within one session we included individual nested in bout as random effects. Results are shown with Kaplan - Meier survival curves for the latencies to the next behavioural change and were drawn using the packages 'survival' and 'survminer'.

RESULTS

Part 1: Individual Variation in Vigilance and Feeding

We found that the only mediator of individual vigilance was the presence of infants in the group, with the adults in the group with infants showing higher proportions of time spent vigilant than adults in the other groups (Fig. 1a, Table 2, model 1). Neither sex of the focal individual, number of bowls present during the experiment nor the location of the experimental treatment had a substantial impact on the amount of individual vigilance (Table 2, model 1).

Individual feeding was negatively influenced by the presence of young infants in the group (Fig. 1b, Table 2, model 1). Additionally, we found a negative effect of the location, with less feeding in the outside than the inside enclosures (Fig. 1b, Table 2), and a positive effect when two bowls were present (Fig. 1b, Table 2, model 1).

Since there was only one group with infants present in our data set, we reran the model without this group (Grappa) and we found that the negative effect of the outside location and the positive effect of the number of bowls (Appendix Table A3, model 1) on the animals' feeding proportions remained very similar to the effects reported above.

Lastly, our multivariate model revealed a negative correlation between the proportion of time spent vigilant and feeding, although there was great uncertainty associated with this estimate

($r_{\text{individual}}(\text{SE}) = -0.22(0.43)$, 89% CI [-0.83, 0.54]) thus failing to provide compelling evidence for a trade-off between feeding and vigilance. Thus, even though marmosets were unable to feed and be vigilant at the same time, we could not demonstrate a direct trade-off between these individual activities, suggesting that other factors might also have played a role, as for instance coordinating vigilance bouts according to risk levels of the pair mate or low statistical power ($N_{\text{groups}} = 7$).

Part 2: Group Vigilance

To examine whether the marmosets organized their vigilance at the pair level, we compared the observed proportion of time when at least one individual was vigilant to the expected proportion if scanning was independent from the scanning of the pair mate. We found that the observed proportion of time when at least one individual was vigilant was similar to the predicted time (Appendix Fig. A1, Table 2, model 2), suggesting that the animals were scanning independently without synchronizing. The reported model estimates of the difference between predicted and observed group vigilance took potentially confounding effects of presence of infants, the number of bowls and the location into account. Moreover, none of the second-order interaction effects between any of these confounds and the difference between observed versus predicted group vigilance gained strong support from our analyses (Appendix Table A4, model 2 with interactions). We reran this model without the group that had infants and found no change in the results (see Appendix Table A3, model 2).

Part 3: Coordination and Turn Taking of Vigilance and Feeding

To investigate whether marmosets coordinated their vigilance when their pair mate was engaged in an activity that is incompatible with being vigilant, we analysed how vigilance was modulated when the mate was feeding with its head inside the food bowl. Individual vigilance increased during periods when the pair mate of the focal animal was feeding compared to when it was

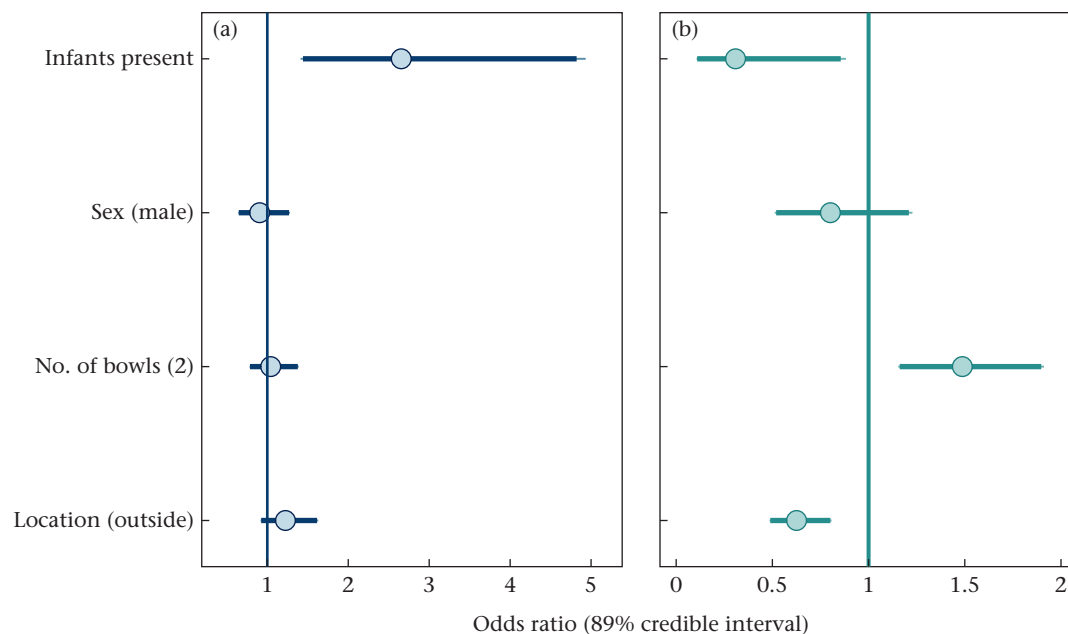


Figure 1. Mediators of variation in individual (a) vigilance and (b) feeding proportions. Posterior interval estimates with medians and 89% credible intervals are shown for different predictors on individual vigilance or feeding rates ($N_{\text{total}} = 56$, $N_{\text{individuals}} = 14$, $N_{\text{groups}} = 7$). Positive effects are visualized with intervals to the right of the vertical line at 1, without the line crossing 1; for negative effects the same holds but intervals are visualized to the left-hand side.

Table 2
Summary of (multivariate) generalized linear mixed-effects models 1–5

| Fixed factors | b (SE) | 67% CI | | 89% CI | | 97% CI | | Pd (%) |
|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|--------------|--------|-------|--------|-------|--------|-------|--------|
| | | Upper | Lower | Upper | Lower | Upper | Lower | |
| Model 1: mediators of individual vigilance and feeding: $R^2_{\mu_{\text{vig}}} = 0.35$, $R^2_{\text{CI}_{\text{vig}}} = 0.18\text{--}0.49$; $R^2_{\mu_{\text{feed}}} = 0.54$, $R^2_{\text{CI}_{\text{feed}}} = 0.38\text{--}0.66$ | | | | | | | | |
| Intercept _{vig} | −0.95 (0.23) | −1.16 | −0.73 | −1.31 | −0.59 | −1.45 | −0.45 | 99.94 |
| Sex _{vig} (male) | −0.10 (0.22) | −0.30 | 0.10 | −0.44 | 0.24 | −0.57 | 0.38 | 69.14 |
| Infants present _{vig} (yes) | 0.98 (0.40) | 0.63 | 1.32 | 0.37 | 1.57 | 0.06 | 1.90 | 98.79 |
| Location _{vig} (outside) | 0.20 (0.17) | 0.04 | 0.37 | −0.08 | 0.48 | −0.17 | 0.58 | 88.10 |
| Bowls _{vig} (2) | 0.04 (0.17) | −0.13 | 0.21 | −0.24 | 0.32 | −0.33 | 0.42 | 59.29 |
| Intercept _{feed} | −0.88 (0.31) | −1.15 | −0.60 | −1.35 | −0.41 | −1.58 | −0.19 | 99.41 |
| Intercept Zi _{feed} | −9.03 (3.53) | −12.24 | −5.78 | −15.28 | −4.56 | −18.89 | −3.63 | 99.93 |
| Zi _{feed} infants (yes) | 4.33 (3.37) | 1.25 | 7.51 | −0.90 | 9.79 | −3.19 | 11.95 | 91.23 |
| Sex _{feed} (male) | −0.23 (0.27) | −0.47 | 0.01 | −0.65 | −0.19 | −0.87 | 0.39 | 82.08 |
| Infants present _{feed} (yes) | −1.18 (0.67) | −1.77 | −0.58 | −2.22 | −0.16 | −2.72 | 0.39 | 96.39 |
| Location _{feed} (outside) | −0.47 (0.15) | −0.62 | −0.32 | −0.72 | −0.22 | −0.81 | −0.13 | 99.86 |
| Bowls _{feed} (2) | 0.40 (0.16) | 0.25 | 0.55 | 0.15 | 0.64 | 0.05 | 0.73 | 99.37 |
| Model 2: group vigilance: $R^2_{\mu} = 0.38$, $R^2_{\text{CI}} = 0.22\text{--}0.50$ | | | | | | | | |
| Intercept | −0.12 (0.21) | −0.31 | 0.07 | −0.44 | 0.20 | −0.59 | 0.35 | 72.79 |
| Type of group vigilance (observed) | −0.05 (0.16) | −0.20 | 0.11 | −0.30 | 0.21 | −0.40 | 0.31 | 61.26 |
| Infants present (yes) | 1.14 (0.42) | 0.79 | 1.50 | 0.51 | 1.77 | 0.18 | 2.12 | 99.08 |
| Location (outside) | 0.14 (0.16) | −0.02 | 0.30 | −0.12 | 0.40 | −0.22 | 0.50 | 80.94 |
| Bowls (2) | 0.00 (0.16) | −0.16 | 0.16 | −0.26 | 0.26 | −0.35 | 0.35 | 50.54 |
| Model 3: vigilance during feeding of pair mate: $R^2_{\mu} = 0.37$, $R^2_{\text{CI}} = 0.23\text{--}0.48$ | | | | | | | | |
| Intercept | −0.77 (0.23) | −0.98 | −0.57 | −1.12 | −0.42 | −1.30 | −0.28 | 99.83 |
| Context (during feeding) | 0.25 (0.14) | 0.12 | 0.47 | 0.03 | 0.47 | −0.05 | 0.56 | 96.60 |
| Infants present (yes) | 0.94 (0.49) | 0.51 | 1.37 | 0.17 | 1.69 | −0.21 | 2.09 | 96.96 |
| Location (outside) | 0.14 (0.14) | 0.01 | 0.28 | −0.08 | 0.36 | −0.16 | 0.44 | 84.64 |
| Bowls (2) | −0.06 (0.14) | −0.19 | 0.08 | −0.27 | 0.16 | −0.35 | 0.23 | 66.00 |
| Model 4: overall coordination of vigilance and feeding: $R^2_{\mu} = 0.57$, $R^2_{\text{CI}} = 0.41\text{--}0.67$ | | | | | | | | |
| Intercept | −0.60 (0.33) | −0.89 | −0.31 | −1.11 | −0.09 | −1.37 | 0.14 | 96.50 |
| Type of simultaneous feeding (observed) | −0.02 (0.16) | −0.18 | 0.13 | −0.28 | 0.23 | −0.38 | 0.32 | 56.39 |
| Infants present (yes) | −1.57 (0.89) | −2.35 | −0.82 | −2.95 | −0.23 | −3.57 | 0.55 | 96.33 |
| Location (outside) | −0.48 (0.17) | −0.65 | −0.31 | −0.76 | −0.21 | −0.86 | −0.11 | 99.65 |
| Bowls (2) | −0.10 (0.17) | −0.26 | 0.06 | −0.36 | 0.17 | −0.46 | 0.27 | 72.22 |
| Model 5: turn taking vigilance and feeding | | | | | | | | |
| Intercept | 1.80 (0.44) | 1.40 | 2.20 | 1.12 | 2.49 | 0.83 | 2.80 | 99.96 |
| Type of interval | | | | | | | | |
| Opposite versus matched | −0.08 (0.05) | −0.13 | −0.04 | −0.16 | −0.01 | −0.19 | 0.02 | 95.83 |
| Co-feeding versus co-vigilance | 0.10 (0.10) | 0.00 | 0.20 | −0.07 | 0.26 | −0.13 | 0.32 | 83.82 |
| Reference individual (male) | 0.19 (0.14) | 0.06 | 0.32 | −0.03 | 0.41 | −0.11 | 0.49 | 91.67 |
| Location (outside) | 0.38 (0.15) | 0.24 | 0.52 | 0.14 | 0.62 | 0.05 | 0.71 | 99.53 |
| Bowls (2) | 0.22 (0.15) | 0.07 | 0.36 | −0.02 | 0.46 | −0.10 | 0.54 | 93.44 |
| Reference interval interrupted (yes) | −1.03 (0.20) | −1.22 | −0.84 | −1.35 | −0.71 | −1.46 | −0.61 | 100.00 |

CI: Bayesian credible interval; pd: probability of direction; R^2 : Bayesian version of the R^2 statistic; zi: zero-inflation.

not (Fig. 2a, Table 2, model 3). Again, this difference was not moderated by the presence of infants, the location and, most importantly, the number of bowls (Appendix Fig. A2a, b, Table A4, model 3 with interactions). The latter result is crucial because it shows that the increase in vigilance occurred regardless of whether one or two bowls were available. The increase in vigilance can thus not be an artefact of restricted space to feed simultaneously when only one bowl was available, but the animals were indeed coordinating their vigilance. The same, but slightly weaker pattern was found in the smaller data set when excluding the group with infants (Grappa; Appendix Table A3, model 3).

To corroborate this finding and further investigate to what extent the animals engaged in turn taking, we focused on the situation when both animals were sitting on the feeding basket containing the food bowls. In particular, we analysed whether individuals would not only adjust to the feeding of the pair mate overall by increasing vigilance when the mate was feeding, but also minimize overlapping feeding times when feeding simultaneously on the feeding basket, and thus take turns feeding. We therefore compared the predicted simultaneous feeding rates under the assumption of independent feeding with the observed rate of simultaneous feeding. The rate of simultaneous feeding was found to be slightly lower than the predicted rates, but these estimates were very uncertain (Appendix Fig. A2c, Table 2, model 4). This

result stayed very similar when excluding the group with infants (Grappa; Appendix Table A3, model 4). To further examine the behaviour on the feeding basket we wanted to assess whether, at any point in time, an individual was more likely to change its behaviour (i.e. had a higher proportional hazards ratio) whenever its social partner was engaged in the same (co-feeding or co-vigilance) behaviour, compared to when its partner showed the opposite behaviour (thus one individual feeding and the other being vigilant or vice versa). Indeed, we found that individuals were faster to change their behaviour if both partners were doing the same (co-feeding or co-vigilance), and intervals with opposite behavioural states lasted longer ($HR_{\text{opposite vs matched intervals}} = 0.92$; Fig. 2b, Table 2, model 5). This result is further consistent with turn taking because, again, this pattern was not driven by the number of bowls available (Appendix Table A4, model 5 with interactions). The results were consistent (although similar to model 3, they were a bit weaker) when excluding the group with infants (Grappa) from the analysis (Appendix Table A3, model 5).

DISCUSSION

This study investigated predictors of individual variation in anti-predator vigilance and feeding along with the ability to take social information into account in regulating these behaviours in captive

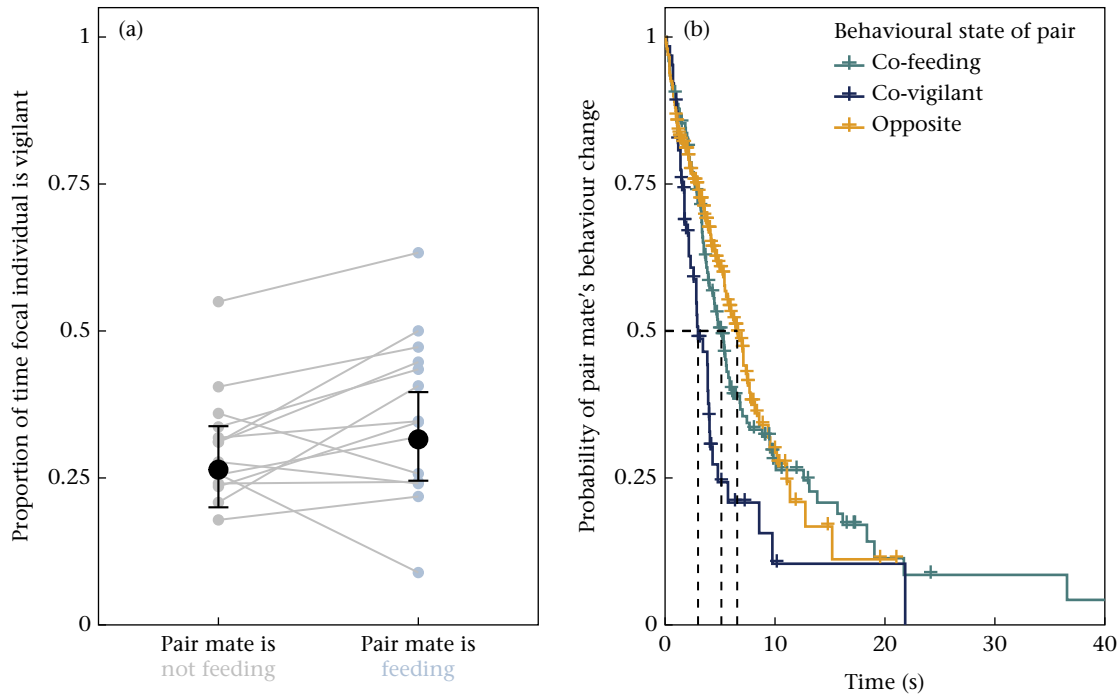


Figure 2. Coordination of vigilance and feeding. (a) Vigilance coordination in response to the pair mate's risk level: comparison between the proportion of time individuals were vigilant during nonfeeding versus feeding periods of the pair mate ($N_{\text{total}} = 110$, $N_{\text{individuals}} = 14$, $N_{\text{groups}} = 7$). Median model estimates with 89% Bayesian credible intervals are shown in black. Raw means by individual are indicated by circles connected by lines. (b) The probability of the pair mate's behavioural change not yet having occurred when individuals were performing the same (co-feeding or co-vigilance) or opposite behaviours (Kaplan - Meier curves). $N = 386$ with 159 censored events. Dashed lines indicate median survival (opposite = 6.56 s, co-feeding = 5.12 s, co-vigilance = 3.00 s).

common marmosets. We used a two-by-two design with varying locations and number of feeding bowls provided. This set-up allowed us to control for varying degrees of riskiness in the environment (outside enclosures are likely to be perceived as more dangerous, since birds of prey, planes, etc. are much more visible) as well as to exclude effects of available feeding space on the possibility of coordination of feeding and vigilance. Our results suggest that marmoset vigilance is remarkably flexible, revealing patterns of coordinated turn taking by taking the risk levels of a conspecific into account and coordinating their vigilance accordingly.

In part 1 of this study, we found a strong positive effect of the presence of infants on individuals' vigilance and a negative effect on feeding behaviour. Even though this effect is statistically very pronounced we only had one group with infants present in the current data set. This is a clear limitation of our study and requires replication in a larger data set since this group might be inherently different from the others. Nevertheless, the effects of infants are in line with previous studies on callitrichid vigilance (below). The location of the experimental treatment (inside versus outside) did not affect vigilance behaviour but did affect feeding (i.e. less feeding outside), which was also positively affected by the presence of a second bowl. Animals were not used to being fed their morning mash in the outside enclosure, which might have influenced these results, and, thus, including groups that are familiar with being fed outside for the mash feeding could have been an additional improvement in terms of our design. The strong opposite effect of the presence of small and vulnerable infants (1–4 weeks old), which are carried most of the time, on the overall feeding and vigilance proportions confirmed our predictions and corroborates the validity of our experimental set-up by showing that antipredator vigilance plays a major role in marmosets' behavioural repertoire even in captivity. Studies on captive cottontop tamarins reveal similarly that when infants are present feeding behaviour is

reduced especially in fathers and generally individuals carrying the infants (Price, 1992; Sánchez et al., 1999). Furthermore, male cottontop tamarins have been reported to lose a significant amount of weight during the first weeks of the infants' life (this is especially prominent in groups with no helpers which corresponds to the situation in the group with infants; Achenbach & Snowdon, 2002).

Adjusting vigilance levels when infants are born corroborates marmosets' vigilance as a behaviour that is not exclusively selfish. A similar effect has also been found in wild black howler monkeys, *Alouatta pigra*, where group members increased their vigilance levels after the birth of infants (Treves et al., 2001; for a study in birds see: Xu et al., 2020) as well as an increased vigilance in mothers with dependent infants specifically (Boinski et al., 2003; Treves, 2003). For cooperatively breeding callitrichids a female-only bias in vigilance related to infants is rather unlikely, and studies have instead found a male bias in general vigilance activities (Gosselin-Ildari & Koenig, 2012; Koenig, 1998; Stojan-Dolar & Heymann, 2010), which we did not find in the present study. A recent review of antipredator behaviours in primates argues that vigilance is an example of 'acts of assistance' by males towards females and their young (van Schaik et al., 2021). Such acts would be rather straightforward in the case of cooperative breeders, in which males contribute significantly to parental duties (Erb & Porter, 2017), not least since females incur very high energetic costs due to twinning and postpartum oestrus (Beehner & Lu, 2013; Leutenegger, 1973, 1979). An increase in vigilance in mothers only is thus rather unlikely (for further elaboration on these sex effects in callitrichids see the Appendix).

Part 2 of our analysis showed that marmoset pairs neither synchronized nor coordinated their vigilance at the group level but it did show that the vigilance was independent at the level of the pair and that this effect was not mediated by the location of the experimental session, the number of bowls available or the

presence of infants. The easiest way vigilance can become synchronized across individuals is when external events simultaneously trigger the same vigilance response in all animals (Blanchard & Fritz, 2007; Ruxton & Roberts, 1999). This explanation is very hard to exclude especially in environments in which animals have little control over what they are experiencing, as in the wild. In contrast to these studies, the captive setting with its controlled predictability can be seen as an advantage. In fact, external 'zeitgebers' are particularly unlikely to have been influencing our results for two main reasons: (1) we a priori excluded time periods with obvious external influences that could potentially trigger vigilance in all animals simultaneously and (2) we did not find a difference in the amount of group vigilance between the outside and inside locations of the experiment. Our results thus suggest that during quiet periods without major disturbances, marmosets do not synchronize their vigilance spontaneously.

Our findings also suggest no coordination of vigilance, which would lead to a sentinel-like system. Arguably, such systems most likely emerge when overall threat levels are chronically high and induce strong trade-offs for the individuals between their own feeding and the necessity of being vigilant. Such trade-offs at the individual level were not present in our data from captive marmosets (see part 1). To investigate whether this is an artefact of captivity, where vigilance is still high but real, chronic threat levels are much lower than in the wild, it would be highly desirable to complement our findings with data from free-ranging marmosets. We predict that coordination, and thus sentinel-like systems, are more likely to emerge whenever individuals face chronically high predation pressure and start experiencing strong trade-offs between the need to be vigilant and other survival-relevant activities.

Part 3 of our study indicates that although marmosets' vigilance is not generally organized at the group level it can be more flexibly adapted to specific contexts of danger, notably not to the individuals' own risk levels but that of their pair mates. We have shown that individuals increased their vigilance during periods when their pair mate was feeding and could not be vigilant themselves, likely indicating that the lack of attention towards the surroundings during a feeding bout, and thus the animal's increased vulnerability, can still induce higher vigilance levels in the partner that is not feeding. Crucially the increase in vigilance occurred regardless of whether there were one or two bowls available to the pair. Thus, this increase in vigilance cannot solely be an artefact of restricted space to feed simultaneously when only one bowl was available. Furthermore, we did not include gaze directed towards the conspecific (often called social monitoring, Allan & Hill, 2018) in our measure of antipredator vigilance. Hence, the increase in vigilance during a feeding bout of a pair mate was also not driven by increased attention towards the other group member either to assess whether the feeding bowl was accessible or due to general food competition. An alternative explanation would be that marmosets were increasing their vigilance levels while the pair mate was feeding to minimize periods during which neither individual was vigilant, and thus exhibiting rather selfish motivations, while still taking the vigilance level of others into account (which would be expected for coordinated vigilance, Beauchamp, 2015). Since we did not find any evidence for a general pattern of coordination when looking at vigilance overall (see part 2), this explanation is rather unlikely. Our results therefore suggest that the marmosets show true, prosocial coordination of vigilance.

This coordination, likely due to a sensitivity to others' vulnerability, is also found in different contexts such as during food sharing. Callitrichids are known to share more food when food is scarce (de Oliveira Terceiro, 2021) or more difficult to access

(again taking the needs of others into account; lion tamarins: Moura et al., 2010; cottontop tamarins: Humle & Snowdon, 2008, marmosets: Martins & Burkart, 2013). Moreover, they adjust their food sharing to the presence or absence of other group members that are available to potentially share food, and thus show an awareness of the amount of help available in a certain context (Brügger et al., 2018). Furthermore, when their prosocial behaviours in general are analysed, the criteria used for intentionality in communication research are also met. Marmoset prosociality is flexible, as shown by audience effects and goal-directedness, indicating that marmosets' cooperative actions are under some degree of voluntary control (Burkart & van Schaik, 2020). With this study we add to this evidence by providing another context in which marmosets adjust their behaviour to the needs of conspecifics, namely the need for vigilance because when feeding from bowls they cannot see anything themselves. This flexibility is even more remarkable in light of the difference in risk level between bowl feeding and the natural feeding behaviour of marmosets, which does not pose a particular risk as wild marmosets can mostly, but not exclusively (e.g. gauging from tree holes, removing insects from crevices, van Schaik & van Noordwijk, 1989), feed upright and thus be vigilant at the same time. Our study also extends the evidence that marmosets are particularly in tune with their social surroundings in general, as they have recently been shown to socially evaluate conspecifics' third-party interactions (Brügger et al., 2021).

Lastly, our analyses of situations when both animals were on the feeding basket suggest turn taking. (1) We found a very small difference in predicted and observed probabilities of simultaneous feeding on the feeding basket, indicating that the animals were mostly not coordinating their feeding bouts overall. However, (2) the more detailed analysis on Kaplan - Meier survival curves of all possible co-occurrences of behavioural states revealed that when animals were performing opposite behaviours, it took them longer to change their behaviour than when pair mates performed the same behaviours, suggesting individuals were taking turns. Overall, these results confirm our spontaneous observations of turn taking in feeding and vigilance on the feeding basket (see [Supplementary video S1](#)). At the same time, however, the pattern is not very strong. This might seem surprising considering the feeding basket was situated at the front of the enclosure, which, especially in the outside location, is arguably the most exposed position within the enclosure. A possible explanation for the lack of stronger evidence for turn taking could be that the level of riskiness was already gauged before both individuals decided to feed on the basket at the same time and, after this decision had been made, any further coordination would be a costly behaviour that can be avoided. Another very likely explanation is that the data available did not allow for enough statistical power since the time both freely moving animals spent on the feeding basket was limited.

Investigations on vigilance have a long tradition in behavioural research and especially primatology. The focus has been mostly on group size effects or general patterns that influence vigilance behaviour (sex, dominance status, age, etc., Allan & Hill, 2018). Our study highlights that vigilance behaviour can provide valuable insight into questions of cooperation and cognition. The set-up of the study, namely a feeding situation where feeding and being vigilant are mutually exclusive, is artificial in the sense that common marmosets in the wild do not feed as frequently with their head fully covered. The fact that they can adjust their vigilance in a rather artificial setting provides further evidence that their vigilance behaviour is considerably flexible. Yet we fully acknowledge that this study has a limited sample size and thus the patterns found need replication. Further studies investigating the mechanisms responsible for coordination patterns would be very

valuable. Computer vision and noninvasive technology to automatically track gaze directions and allow for a finer grained analysis of how animals are organizing their threat detection and group life more generally could help unveil what exactly animals understand about the risk levels of others and how close this understanding is to human theory of mind abilities.

Author Contributions

R.K. Brügger: conceptualization, methodology, investigation, formal analysis, visualization, data curation, writing – original draft, writing – review & editing, project administration, funding acquisition. **E.P. Willems:** methodology, formal analysis, writing – review & editing. **J.M. Burkart:** conceptualization, methodology, resources, writing – review & editing, supervision, project administration, funding acquisition.

Data Availability

All relevant data are available on OSF at <https://doi.org/10.17605/OSF.IO/XDK4Z>.

Declaration of Interest

The authors do not have any competing interests.

Acknowledgments

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Supplementary Material

Supplementary material associated with this article is available, in the online version, at <https://doi.org/10.1016/j.anbehav.2022.11.007>.

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Appendix

Additional Methods: Statistical Analysis

Model parameters were estimated by running four independent Monte Carlo Markov Chains for up to 10 000 iterations, with the first half used as 'warmup' of the algorithm and the second half to sample the posterior distribution. To aid model convergence, the explored parameter space was probabilistically restricted by weakly regularizing priors (McElreath, 2016). We specified normal distributions ($\mu = 0$, $\sigma = 10$ and $\mu = 0$, $\sigma = 5$, respectively) for fixed intercepts and slopes, and a Cauchy distribution ($x_0 = 0$, $\gamma = 2$) for random intercepts, as well as a Lewandowski–Kurowicka–Joe (LKJ) distribution for the correlation between the two outcome variables ($\eta = 2$). To ensure chains had properly mixed, converged and were stationary, we visually inspected trace plots, made sure R-hat values equalled one ($\hat{R} = 1.00$), and insisted on effective sample sizes greater than 2000. We increased the value of the 'adapt_delta' argument in the 'brm()' function to 0.99, while allowing a maximal tree depth of 16, to achieve this for all models.

Sex Effects on Vigilance

The evidence for sex effects on vigilance behaviour even in callitrichids is not indisputable. A study by Smith et al. (2004) also failed to show a sex effect in two species of tamarins in the wild. They argued that the difference in the visual system with some females being trichromatic and some dichromatic, as are all males, would be able to influence predator perception and consequently interfere with measured sex effects on vigilance levels. Another option would be that vigilance in the setting of this study is not costly enough and thus males are not needed to provide additional support or that methodological differences between studies are still too big to allow definitive conclusions. Lastly, those acts of service could become much more relevant in a setting where threat levels are higher. In our study, we found some evidence that marmosets perceived the outside location as more dangerous by showing lower feeding rates outside than inside. Nevertheless, we did not find any evidence of higher vigilance rates outside for either sex. Thus, more research, especially in the wild where predation pressures are higher and much more variable, is needed to determine the relevance of acts of assistance by males.

Table A1
Individuals participating in the study

| Group | Individual | Sex | Status | Birth date | Conditions (in order of testing) |
|-----------|------------|-----|---------|--------------|-------------------------------------|
| Garetta | Garetta | F | Breeder | 11 June 2009 | I2; O2; O1; I1 |
| | Nuno | M | Breeder | 23 May 2013 | |
| Gaviota | Gaviota | F | Breeder | 03 Oct 2006 | O1; O2; I2; I1 |
| | Kapi | M | Breeder | 01 Sept 2002 | |
| Grappa | Grappa | F | Breeder | 17 Mar 2015 | O1; O2; I1; I2 (No vigilance coded) |
| | Craken | M | Breeder | 10 Oct 2013 | (No vigilance coded) |
| | Ginger | F | Infant | 04 May 2018 | |
| | Guapa | F | Infant | 04 May 2018 | |
| Greta | Greta | F | Breeder | 11 Oct. 2011 | I1; O1; O2; I2 |
| | Mars | M | Breeder | 11 July 2012 | |
| Lilly | Lilly | F | Breeder | 03 July 2012 | I1; O1; I2; O2 |
| | Nando | M | Breeder | 23 May 2013 | |
| Vesta | Vesta | F | Helper | 05 Oct 2004 | O2; O1; I2; I1 |
| | Vito | M | Helper | 30 May 2006 | |
| Wisconsin | Wisconsin | F | Breeder | 30 Aug 2013 | O2; I1; I2; O2 |
| | Tabor | M | Breeder | 30 Oct 2008 | |

F: female; M: male; I: inside; O: outside; 1: one food bowl; 2: two food bowls. Data collection period: 3–31 May 2018.

Table A2
Duration of session for each group including total duration of invalid periods

| Group | Session | Total length (min:s) | Invalid periods (min:s) |
|-----------|---------|----------------------|-------------------------|
| Garetta | I2 | 10:12 | 0 |
| Garetta | O2 | 10:00 | 0 |
| Garetta | O1 | 10:34 | 0 |
| Garetta | I1 | 07:15 | 0 |
| Gaviota | O1 | 10:00 | 0 |
| Gaviota | O2 | 09:12 | 04:54 |
| Gaviota | I2 | 04:59 | 0 |
| Gaviota | I1 | 08:36 | 0 |
| Grappa | O1 | 10:14 | 00:50 |
| Grappa | O2 | 14:04 | 04:03 |
| Grappa | I1 | 21:26 | 11:20 |
| Grappa | I2 | 10:00 | 0 |
| Greta | I1 | 05:13 | 0 |
| Greta | O1 | 04:35 | 0 |
| Greta | O2 | 05:48 | 0 |
| Greta | I2 | 05:26 | 02:40 |
| Lilly | I1 | 08:46 | 0 |
| Lilly | O1 | 04:53 | 0 |
| Lilly | I2 | 08:35 | 0 |
| Lilly | O2 | 10:11 | 0 |
| Vesta | O2 | 05:38 | 0 |
| Vesta | O1 | 04:11 | 0 |
| Vesta | I2 | 4:06 | 0 |
| Vesta | I1 | 6:12 | 02:30 |
| Wisconsin | O2 | 6:37 | 0 |
| Wisconsin | I1 | 10:29 | 0 |
| Wisconsin | I2 | 6:48 | 0 |
| Wisconsin | O2 | 6:44 | 0 |

I: inside; O: outside; 1: one food bowl; 2: two food bowls.

Table A3

Summary of generalized linear mixed-effects models 1–5 without the group Grappa (only group with infants)

| Fixed factors | b (SE) | 67% CI | | 89% CI | | 97% CI | | Pd (%) |
|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|--------------|--------|-------|--------|-------|--------|-------|--------|
| | | Upper | Lower | Upper | Lower | Upper | Lower | |
| Model 1: mediators of individual vigilance and feeding: $R^2_{\mu_{\text{vig}}} = 0.21$, $R^2_{\text{CI}_{\text{vig}}} = 0.05$ –0.38; $R^2_{\mu_{\text{feed}}} = 0.45$, $R^2_{\text{CI}_{\text{feed}}} = 0.24$ –0.60 | | | | | | | | |
| Intercept _{vig} | –0.83 (0.23) | –1.05 | –0.62 | –1.18 | –0.47 | –1.33 | –0.31 | 99.83 |
| Sex _{vig} (male) | –0.02 (0.23) | –0.23 | 0.19 | –0.39 | 0.34 | –0.53 | 0.50 | 54.01 |
| Location _{vig} (outside) | –0.05 (0.16) | –0.21 | 0.11 | –0.31 | 0.21 | –0.41 | 0.32 | 61.31 |
| Bowls _{vig} (2) | –0.06 (0.17) | –0.22 | 0.10 | –0.33 | 0.20 | –0.42 | 0.29 | 64.76 |
| Intercept _{feed} | –0.89 (0.23) | –1.18 | –0.60 | –1.39 | –0.40 | –1.61 | –0.16 | 99.36 |
| Sex _{feed} (male) | –0.21 (0.31) | –0.49 | 0.05 | –0.69 | 0.27 | –0.91 | 0.52 | 78.38 |
| Location _{feed} (outside) | –0.42 (0.17) | –0.58 | –0.27 | –0.69 | –0.16 | –0.79 | –0.06 | 99.36 |
| Bowls _{feed} (2) | 0.38 (0.17) | 0.22 | 0.54 | 0.11 | 0.65 | 0.01 | 0.75 | 98.66 |
| Model 2: group vigilance: $R^2_{\mu} = 0.19$, $R^2_{\text{CI}} = 0.03$ –0.36 | | | | | | | | |
| Intercept | 0.05 (0.21) | –0.14 | 0.23 | –0.27 | 0.37 | –0.42 | 0.53 | 60.16 |
| Type of group vigilance (observed) | –0.01 (0.15) | –0.15 | 0.13 | –0.25 | 0.22 | –0.33 | 0.31 | 53.56 |
| Location (outside) | –0.05 (0.15) | –0.20 | 0.09 | –0.29 | 0.19 | –0.39 | 0.28 | 64.08 |
| Bowls (2) | –0.12 (0.15) | –0.26 | 0.03 | –0.35 | 0.12 | –0.44 | 0.21 | 78.32 |
| Model 3: vigilance during feeding of pair mate: $R^2_{\mu} = 0.37$, $R^2_{\text{CI}} = 0.23$ –0.48 | | | | | | | | |
| Intercept | –0.69 (0.21) | –0.88 | –0.49 | –1.02 | –0.36 | –1.17 | –0.20 | 99.72 |
| Context (during feeding) | 0.21 (0.14) | 0.07 | 0.34 | –0.01 | 0.43 | –0.10 | 0.50 | 93.21 |
| Location (outside) | –0.02 (0.14) | –0.15 | 0.11 | –0.24 | 0.20 | –0.32 | 0.29 | 55.85 |
| Bowls (2) | –0.14 (0.14) | –0.28 | –0.01 | –0.36 | 0.08 | –0.45 | 0.16 | 85.47 |
| Model 4: overall coordination of vigilance and feeding: $R^2_{\mu} = 0.51$, $R^2_{\text{CI}} = 0.32$ –0.63 | | | | | | | | |
| Intercept | –0.55 (0.33) | –0.84 | –0.25 | –1.07 | –0.03 | –1.33 | 0.21 | 95.41 |
| Type of simultaneous feeding (observed) | 0.01 (0.16) | –0.15 | 0.16 | –0.25 | 0.26 | –0.36 | 0.36 | 51.81 |
| Location (outside) | –0.47 (0.17) | –0.64 | –0.31 | –0.76 | –0.19 | –0.85 | –0.10 | 99.62 |
| Bowls (2) | –0.15 (0.17) | –0.31 | 0.01 | –0.42 | 0.12 | –0.52 | 0.22 | 81.69 |
| Model 5: turn taking vigilance and feeding | | | | | | | | |
| Intercept | 1.61 (0.49) | 1.16 | 2.06 | 0.84 | 2.38 | 0.54 | 2.72 | 99.88 |
| Type of interval | | | | | | | | |
| Unmatched versus matched | 0.27 (0.21) | 0.07 | 0.47 | –0.07 | 0.60 | –0.19 | 0.72 | 89.72 |
| Co-feeding versus co-vigilance | –0.08 (0.16) | –0.24 | 0.08 | –0.34 | 0.18 | –0.44 | 0.28 | 68.91 |
| Reference individual (male) | 0.16 (0.14) | 0.02 | 0.30 | –0.07 | 0.39 | –0.15 | 0.47 | 86.76 |
| Location (outside) | 0.41 (0.15) | 0.26 | 0.55 | 0.16 | 0.65 | 0.08 | 0.73 | 99.63 |
| Bowls (2) | 0.28 (0.16) | 0.13 | 0.43 | 0.03 | 0.53 | –0.06 | 0.62 | 96.36 |
| Reference interval interrupted (yes) | –0.99 (0.20) | –1.19 | –0.80 | –1.32 | –0.67 | –1.45 | –0.56 | 100 |

CI: Bayesian credible interval; pd: probability of direction. R^2 : Bayesian version of the R^2 statistic.

Table A4
Summary of generalized linear mixed-effects models 2, 3 and 5 with interactions

| Fixed factors | b (SE) | 67% CI | | 89% CI | | 97% CI | | Pd (%) |
|-------------------------------------------------------------|--------------|--------|-------|--------|-------|--------|-------|--------|
| | | Upper | Lower | Upper | Lower | Upper | Lower | |
| Model 2 with interactions | | | | | | | | |
| Intercept | −0.08 (0.24) | −0.30 | 0.15 | −0.45 | 0.30 | −0.61 | 0.46 | 62.89 |
| Type of group vigilance (observed) | 0.04 (0.29) | −0.24 | 0.32 | −0.42 | 0.51 | −0.58 | 0.68 | 55.12 |
| Infants present (yes) | 1.03 (0.49) | 0.59 | 1.47 | 0.29 | 1.79 | −0.02 | 2.14 | 98.39 |
| Location (outside) | 0.14 (0.23) | −0.09 | 0.36 | −0.23 | 0.51 | −0.37 | 0.64 | 72.55 |
| Bowls (2) | −0.06 (0.23) | −0.28 | 0.17 | −0.43 | 0.32 | −0.56 | 0.45 | 59.38 |
| Type of group vigilance (observed)*infants present (yes) | −0.29 (0.53) | −0.80 | 0.22 | −1.12 | 0.55 | −1.45 | 0.87 | 71.40 |
| Type of group vigilance (observed)*location (outside) | 0.00 (0.33) | −0.32 | 0.32 | −0.53 | 0.54 | −0.72 | 0.73 | 50.29 |
| Type of group vigilance (observed)*bowls (2) | −0.11 (0.33) | −0.43 | 0.21 | −0.64 | 0.42 | −0.84 | 0.61 | 62.49 |
| Model 3 with interactions | | | | | | | | |
| Intercept | −0.78 (0.25) | −1.01 | −0.55 | −1.18 | −0.39 | −1.34 | −0.21 | 99.61 |
| Context (during feeding) | 0.24 (0.26) | −0.01 | 0.48 | −0.18 | 0.65 | −0.32 | 0.80 | 82.53 |
| Infants present (yes) | 1.12 (0.54) | 0.65 | 1.60 | 0.29 | 1.95 | −0.12 | 2.33 | 97.80 |
| Location (outside) | 0.10 (0.20) | −0.09 | 0.29 | −0.22 | 0.41 | −0.33 | 0.52 | 68.87 |
| Bowls (2) | −0.05 (0.19) | −0.24 | 0.14 | −0.36 | 0.27 | −0.47 | 0.37 | 59.78 |
| Context (during feeding)*infants present (yes) | 0.37 (0.40) | −0.02 | 0.76 | −0.27 | 1.02 | −0.49 | 1.26 | 82.41 |
| Context (during feeding)*location (outside) | −0.09 (0.28) | −0.36 | 0.18 | −0.54 | 0.36 | −0.71 | 0.52 | 62.66 |
| Context (during feeding)*bowls (2) | 0.02 (0.28) | −0.25 | 0.29 | −0.42 | 0.46 | −0.59 | 0.63 | 52.72 |
| Model 5 with interactions | | | | | | | | |
| Intercept | 1.86 (0.46) | 1.43 | 2.28 | 1.16 | 2.57 | 0.86 | 2.89 | 99.98 |
| Type of interval | | | | | | | | |
| Unmatched versus matched | −0.15 (0.11) | −0.25 | −0.04 | −0.32 | 0.02 | −0.38 | 0.08 | 92.02 |
| Co-feeding versus co-vigilance | 0.27 (0.21) | 0.07 | 0.48 | −0.07 | 0.61 | −0.20 | 0.72 | 90.39 |
| Reference individual (male) | 0.04 (0.15) | −0.10 | 0.19 | −0.20 | 0.29 | −0.29 | 0.38 | 61.26 |
| Location (outside) | 0.40 (0.16) | 0.24 | 0.56 | 0.15 | 0.67 | 0.05 | 0.76 | 99.44 |
| Bowls (2) | 0.29 (0.16) | 0.13 | 0.44 | 0.03 | 0.54 | −0.06 | 0.63 | 96.62 |
| Reference interval interrupted (yes) | −1.06 (0.20) | −1.25 | −0.86 | −1.38 | −0.74 | −1.51 | −0.63 | 100.00 |
| Type of interval*reference individual | | | | | | | | |
| Unmatched versus matched* reference individual (male) | 0.19 (0.10) | 0.09 | 0.29 | 0.03 | 0.35 | −0.02 | 0.41 | 97.30 |
| Co-feeding versus co-vigilance* reference individual (male) | −0.43 (0.20) | −0.63 | −0.23 | −0.76 | −0.11 | −0.87 | 0.01 | 98.26 |
| Type of interval*location | | | | | | | | |
| Unmatched versus matched* location (outside) | 0.04 (0.10) | 0.06 | 0.14 | −0.12 | 0.20 | −0.18 | 0.26 | 66.67 |
| Co-feeding versus co-vigilance* location (outside) | 0.02 (0.21) | −0.18 | 0.22 | −0.31 | 0.35 | −0.42 | 0.48 | 53.12 |
| Type of interval*bowls | | | | | | | | |
| Unmatched versus matched*bowls (2) | −0.07 (0.10) | −0.17 | 0.02 | −0.23 | 0.08 | −0.28 | 0.14 | 77.81 |
| Co-feeding versus co-vigilance*bowls (2) | 0.06 (0.20) | −0.14 | 0.25 | −0.26 | 0.38 | −0.38 | 0.49 | 61.29 |

CI: Bayesian credible interval; pd: probability of direction.

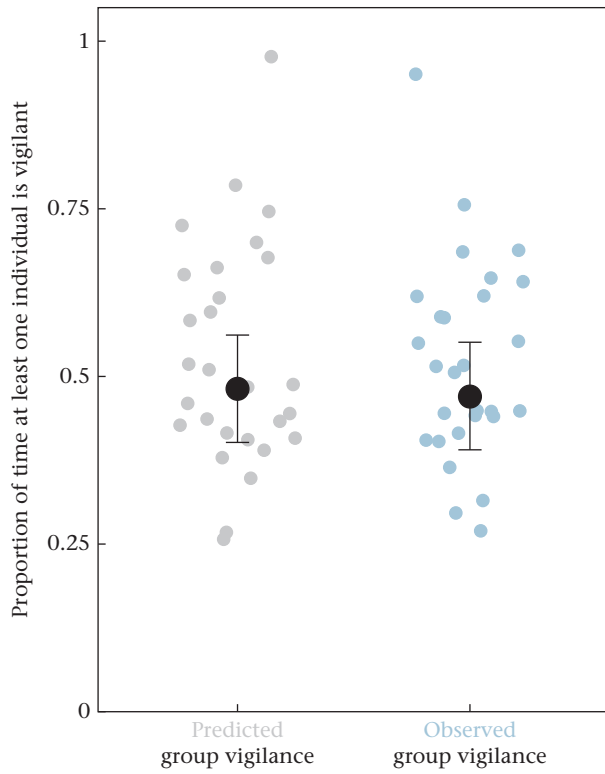


Figure A1. Group vigilance. Comparison between predicted and observed group vigilance calculated as the proportion of time at least one individual was vigilant ($N_{\text{total}} = 56$, $N_{\text{groups}} = 7$). Median model estimates with 89% Bayesian credible intervals are shown in black. Raw values are indicated with grey (predicted) and blue (observed) points.

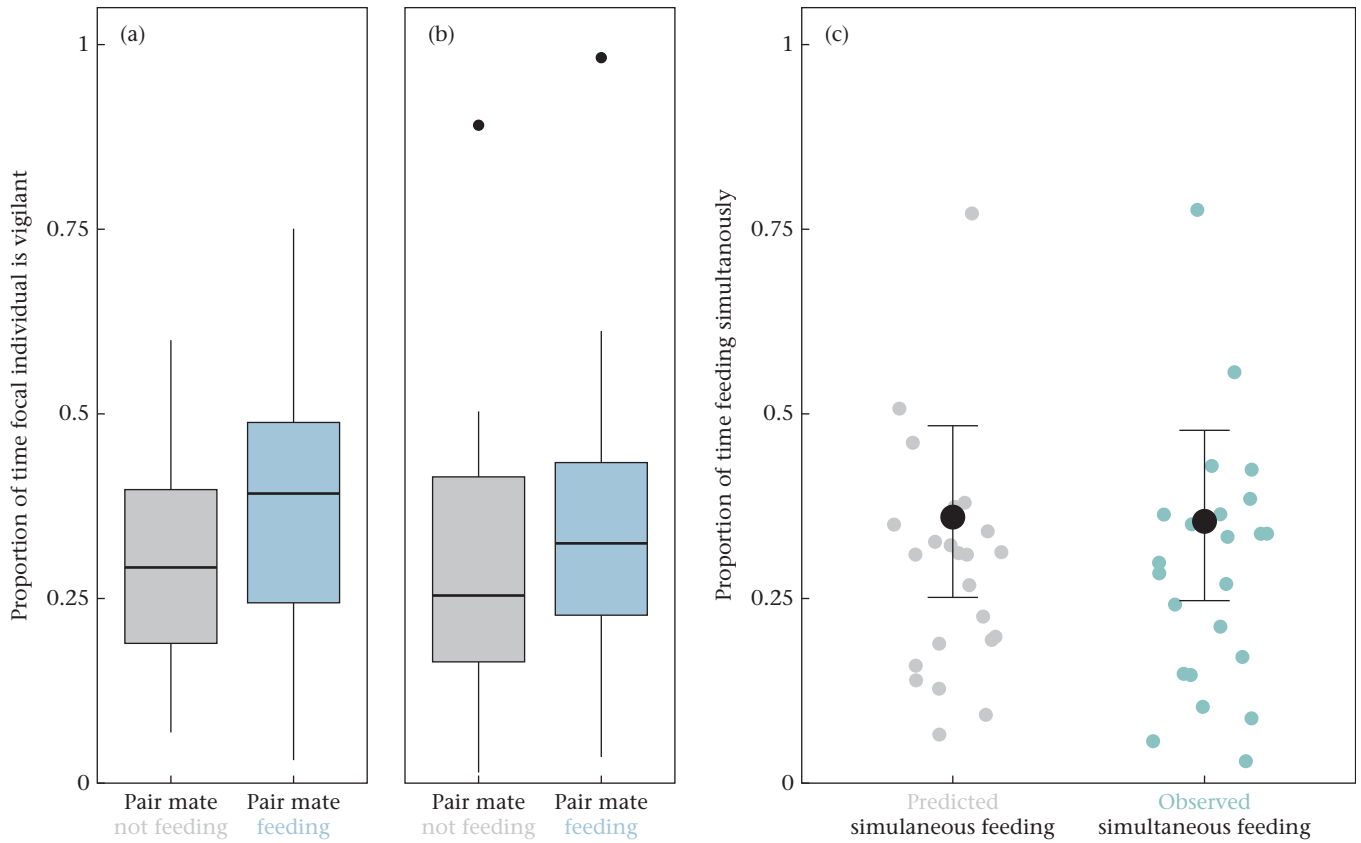


Figure A2. Coordination and turn taking of vigilance and feeding. (a, b) Comparison between proportion of time individuals were vigilant during nonfeeding versus feeding periods of the pair mate split by the number of bowls available: (a) one bowl; (b) two bowls ($N_{\text{total}} = 110$, $N_{\text{individuals}} = 14$, $N_{\text{groups}} = 7$). Box plots are based on raw values. Boxes represent the 25th and 75th percentiles (ends) and the median (centre line); whiskers represent the first quartile $- 1.5 \times$ the interquartile range and the third quartile $+ 1.5 \times$ the interquartile range and all outliers beyond these whiskers are shown. (c) Comparison between predicted and observed proportion of time individuals fed simultaneously ($N_{\text{total}} = 46$, $N_{\text{groups}} = 7$). Median model estimates with 89% Bayesian credible intervals are shown in black. Raw values are indicated with grey (predicted) and blue (observed) points.