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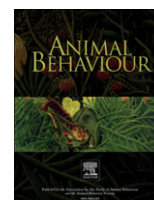
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All together now: behavioural synchrony in baboons

Andrew J. King^{a,b,*}, Guy Cowlshaw^a^a Institute of Zoology, Zoological Society of London^b Evolutionary Ecology Group, Department of Zoology, University of Cambridge, U.K.

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For group-living individuals to remain spatially coherent, coordinated behaviour across group members is essential. We investigated what factors can promote or constrain the achievement of such behavioural synchronization (measured as diversity in activities among group members) in a social primate. Two wild groups of chacma baboons, *Papio ursinus*, were studied in the field by instantaneous scan sampling during full-day follows to test the hypotheses that individual activity budgets, habitat constraints and group properties can all affect patterns of behavioural synchrony. Observed synchrony across individuals was variable, and analysed using a generalized linear mixed model. We found support for each of our three hypotheses. First, the probability of a group being synchronized increased with the number of pregnant females, but decreased with the number of sexually swollen females in a group. Synchrony also declined throughout the day. We interpret these two results in terms of variations in the activity budgets of both sexes related to their reproductive strategies, and changing levels of satiation among individual group members, respectively. Second, synchrony was highest in a 'closed' woodland habitat, and lowest in 'open' desert habitat. This is interpreted as a consequence of habitat differences in food patch configuration and/or predation risk. Third, we found a nonlinear relationship with increasing group cohesion, suggesting that where opportunities for information transfer are limited, behavioural synchrony may be constrained. Overall, our simple approach to quantifying behavioural synchrony highlights the role of both individual variation and the (social and ecological) environment in determining group-level patterns of behaviour.

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Synchronized behaviour occurs when individuals perform activities together in unison, and is a common characteristic of animal aggregations. In some cases, synchrony may be temporally predictable. Famous examples of such rhythmic synchronization are the simultaneous flashing of fireflies on a second-to-second basis (Copeland & Moiseff 1995) and the close synchrony of births in some animal groups across seasons (Gregg et al. 2001; Porter & Wilkinson 2001). In fireflies, synchronized flashing is performed entirely by males and is associated with mating behaviour, which is likely to serve to attract females at a localized level (Otte & Smiley 1977; Ermentrout 1991). In the case of reproductive cycles, birth synchrony can act as a predator-swamping strategy, reducing the predation of vulnerable offspring and increasing the probability of neonate survivorship (Rutberg 1984; Boinski 1987). But behavioural synchrony can also be stochastic, and thus show little temporal predictability. For example, a highly aligned group of animals moving through their environment can be said to have momentarily synchronized their direction of movement (Sumpter

2006). In such cases, the extent of behavioural synchronization at any given moment is most likely to reflect changes in the costs and benefits of realizing this activity synchrony (Rands et al. 2003, 2008).

The benefits of synchrony may be substantial. Behavioural synchrony may be necessary for individuals to maximize the benefits of group living. Take the classic examples of sociality increasing foraging benefits and reducing predation risk. Individuals attempting to find food can increase their opportunity for acquiring social information about the locations and qualities of food resources by foraging at the same time and monitoring the success of others (Fernandez-Juricic et al. 2007; King & Cowlshaw 2007; Valone 2007). Similarly, coordinating antipredator scans among group members can be more efficient than independent scanning (even if individuals must spend a large share of their time coordinating their behaviour) provided that detection information is rapidly shared among group members (Bednekoff & Lima 1998; Rodriguez-Girones & Vasquez 2002). Otherwise, independent scanning may reduce the probability of predator detection because of long gaps where no individuals are vigilant (Ward 1985).

Behavioural synchrony may be costly to achieve, however, for three reasons. First, differences in the optimal activity patterns of

* Correspondence: A. J. King, Institute of Zoology, Zoological Society of London, Regent's Park, London NW1 4RY, U.K.

E-mail address: andrew.king@ioz.ac.uk (A.J. King).

animals of different age or sex can impact on the ability of groups to achieve synchrony. This 'activity-budget hypothesis' has been suggested as an important factor mediating intersexual social segregation and is thought to explain asynchrony in activity between the sexes in many ungulate species (Ruckstuhl 1998; Conradt & Roper 2000; Ruckstuhl & Kokko 2002). However, this hypothesis is not only limited to age–sex classes. Other physiological–morphological characteristics that influence individual state can also impact on nutritional demands (e.g. reproductive state within females: Key & Ross 1999; Barrett et al. 2006) resulting in differences in the duration of foraging bouts and movement rates among individuals, making it costly to remain associated and in synchrony (Rands et al. 2003; Shannon et al. 2008). Indeed, evolutionary game-theory models and more mechanistic models predict that where between-individual variation in the timing of activities becomes too large then synchrony will break down (Sumpter 2006; Conradt & Roper 2007). Second, groups feeding on scattered food resources or moving through particularly heterogeneous habitats may find it difficult to preserve group synchrony. According to this 'habitat-constraints hypothesis', synchrony will break down when all group members are unable to forage together at specific locations (Nonaka & Holme 2007; Vahl et al. 2007; Kazahari & Agetsuma 2008). Third, where group members become visually isolated, or move out of auditory range as a consequence of interneighbour distance, there may be a reduction in behavioural synchrony as a result of reduced opportunity for the use of socially transmitted information via signals or cues (the 'group-structure hypothesis'; see Braune et al. 2005; Cortopassi & Bradbury 2006). Consequently, activity-, habitat- and group-related processes may all contribute to patterns of variability in behavioural synchrony within animal groups.

In this study, we investigated behavioural synchrony for two groups of wild chacma baboons, *Papio ursinus*, in central Namibia. We asked to what degree observed variability in behavioural synchrony can be explained by individual activity budgets (hypothesis H1), habitat constraints (H2) and/or group structure (H3). These hypotheses are not mutually exclusive, and we outline our predictions for each in turn.

In the case of individual activity budgets, female baboons experience changes in energy requirements according to their reproductive state (nonfertile, fertile, pregnant and lactating) and vary their time spent feeding accordingly (Altmann 1980; Dunbar & Dunbar 1988). Higher numbers of females in a single reproductive state are therefore predicted to increase behavioural synchrony, as a consequence of the more homogeneous energy requirements of these females (prediction 1.1). Variation in energetic state among group members is also likely to be smallest in the early morning when all individuals are hungry irrespective of identity (Macleod et al. 2005). In contrast, energetic state and hunger levels will be more variable as the day progresses, as a result of both phenotype-limited foraging success and satiation requirements, caused by differences in age (Heise & Moore 2003; Limmer & Becker 2007), size (Michelena et al. 2006) or dominance (McCormack et al. 2007; Kazahari & Agetsuma 2008; prediction 1.2).

Baboon habitat in our study area falls into two broad categories: rocky desert hills and riparian woodland groves along a dry ephemeral river (King & Cowlshaw 2009a). These two habitats differ along two important axes: food patch configuration (King & Cowlshaw 2009a; King et al. 2009) and predation risk (Cowlshaw 1997a). We expected behavioural synchrony to be higher in the woodland than the desert as a consequence of both these factors. In the case of food patch configuration, where patches are larger and closer together (woodlands) individuals are expected to spend more time feeding in patches and less time either travelling or travel feeding (picking at small food items during locomotion)

between patches. In contrast, in the desert (where patches are smaller and more dispersed), individuals need to distribute their time more evenly across feeding, travel feeding and travelling, leading to lower levels of synchrony (prediction 2.1). Concerning predation risk, Cowlshaw (1997a) suggested that baboons in this population may adopt a time-minimizing strategy, foraging more intensively in areas of higher predation risk to leave those areas as rapidly as possible. Since baboons are at greater risk of predation in woodland (Cowlshaw 1997b), groups might be more highly synchronized in their behaviours to minimize their time spent in this high-risk habitat (prediction 2.2).

Lastly, we expected synchrony to alter according to group properties. We predicted that where groups spread out over a larger area, behavioural synchrony would decrease as a consequence of reduced opportunity for maintaining communication among individuals (Dostalkova & Spinka 2007; prediction 3.1). To test this prediction we explored the effects of group cohesion, calculated as a function of the area occupied by group members and the number of individuals in view. Our two study groups also differed in size. Since larger groups are likely to spread out over wider areas, especially during foraging to reduce intragroup feeding competition (Agetsuma 1995; King et al. 2009, *in press*), we predicted that the larger group will show lower behavioural synchrony than the smaller group (prediction 3.2).

METHODS

Study Site and Subjects

Fieldwork was carried out at Tsaobis Leopard Park, Namibia (22°23'S 15°45'W), on two habituated groups of chacma baboons. There were 22 (18 females, four males) and 14 (10 females, four males) adults from groups containing 57 and 32 individuals (hereafter 'large' and 'small' groups), respectively. All baboons were habituated to direct observation by human observers at close range. Baboons in this semidesert region forage in discrete food patches found in two distinct habitats: riparian woodland and open desert. The riparian woodland occurs in groves along the banks of a dry riverbed and consists mainly of large trees and shrubs (*Prosopis glandulosa*, *Salvadora persica* and *Faidherbia albida*). The open desert, in contrast, is characterized by grasses and scattered dwarf shrubs (mainly *Commiphora virgata*).

Observational Data

At the beginning of each day the reproductive state of each adult female group member was recorded as one of four categories: (1) the nonfertile phase of the oestrous cycle, (2) sexually swollen (the fertile phase of the cycle), (3) pregnant and (4) lactating. The nonfertile and sexually swollen phases of each female were identified by the state of her anogenital skin which, as in many catarrhine primate species, gradually swells during each oestrous cycle, reaching its maximal size around the time of ovulation, before rapidly returning to its nonswollen state. Pregnant females were identified by prolonged nonswollen periods, and a change in colour (to a deep red) of the paracollosal skin. Lactating females were identified by the presence of suckling infants. The proportion of females in each reproductive state could therefore be calculated for each observation day.

Scan sampling at 30 min intervals was also conducted throughout the day. The first scan took place 30 min after the baboon group had left their morning sleeping site, and the last scan was conducted once the group had reached their evening sleeping site shortly before sunset (we thus largely excluded periods at

sleeping sites where individuals were more likely to be resting/grooming and therefore synchronized in their behaviour). A total of 6535 scans across both baboon groups was obtained from 517 days of observations over two field seasons. We conducted 3826 scans in 2005 ($N_{\text{large}} = 1476$, $N_{\text{small}} = 2350$) and 2709 scans in 2006 ($N_{\text{large}} = 1636$, $N_{\text{small}} = 1073$). At each scan, the number of individuals in view was noted (individual identity was not recorded because of the large spread of the group), and the predominant vegetation in which they were ranging was noted as (1) open ground (i.e. mostly absent of vegetation), (2) grasses, (3) shrubs or (4) trees. The first two categories were representative of desert habitat and the latter of woodland habitat. Of the individuals in view, we estimated their distance (m) from front to back (i.e. the distance between the first and last individual with respect to the direction of group travel), a , and from side to side (i.e. the distance between the furthest individuals on either side of the group), b . Initially, distances were recorded using a Bushnell rangefinder with 1 m accuracy at distances of 50–200 m. Once observers could consistently estimate these distances accurately by eye, the rangefinder was used only intermittently. The estimated elliptical area (e) of the group was then calculated as $\pi \times a \times b$. From this, we calculated the group cohesion as the number of baboons in view (v) divided by the area they occupied, that is, v/e . The activity of each individual in view was assigned as either (1) travelling, (2) travel foraging, (3) stationary foraging, (4) resting, (5) grooming or (6) drinking. Travelling was defined as the rapid locomotion of individuals and travel foraging as the slow locomotion of individuals while searching, manipulating and ingesting food material. Stationary foraging described searching, manipulating and ingesting food at a fixed point. Resting was a sedentary state that included sleeping. Grooming was allogrooming between social partners. Drinking described drinking from a water source.

Calculating Synchrony

Since we were concerned with understanding what affects general behavioural synchrony in baboons, we assessed synchrony across a number of broad activity categories (above), and used relatively long sampling intervals of 30 min, while also controlling statistically for the number of individuals in view (see *Analyses of observational data*, below). Specific techniques for quantifying behavioural synchronization have been devised by Engel & Lamprecht (1997) and used to show synchronization of behaviour in ungulates. Such techniques have been used to investigate differences in behavioural synchronization for particular activities between certain individuals or subgroups, for example males and females (Dunbar & Shi 2008), or juveniles and adults (Ruckstuhl 1999). However, such a measure would not work here, where the question of interest was not the degree of concurrence between a focal animal and its neighbour for a particular activity, but rather the group's behavioural synchrony across all individuals and activities. There are other possible approaches: one recent theoretical study, for example, devised a new statistic to assess the proportion of a population that is synchronized at any one moment in time (Rands et al. 2008). However, the authors advised caution against its usefulness in empirical studies, particularly because synchrony was near unity in most of the models they examined. To quantify the degree of behavioural synchrony across whole baboon groups based on all the activities they performed, we therefore used a very simple index that measures diversity in categorical data: the Simpson's Diversity Index (Peet 1974; Krebs 1989).

The behavioural synchrony (B_s) shown by group members at each scan was then calculated as:

$$B_s = \sum_{i=6}^S \frac{n_i(n_i - 1)}{N(N - 1)}$$

where n_i is the number of individuals engaged in a specific activity and N is the total number of individuals in view, for $i = 6$ categories. Values near zero therefore correspond to times where groups are heterogeneous with respect to behaviour and are thus considered asynchronous, whereas values near one represent times when groups are homogeneous with respect to behaviour and are thus synchronous. This statistic has a simple intuitive interpretation: it represents the probability that if two individuals were randomly chosen in the group at a specific time, they would be performing the same behaviour.

Analyses of Observational Data

To investigate whether variability in behavioural synchrony was greater than would be expected by chance, we compared the observed patterns of synchrony with that predicted by a simple model in which each baboon's behaviour was independent of the rest of the group. Each baboon was assigned a probability of performing an activity, based upon the mean proportion of time the baboons spent engaged in each of the six behavioural categories: (1) travelling, (2) travel foraging, (3) stationary foraging, (4) resting, (5) grooming and (6) drinking, derived from scan data for each group. We then simulated each individual's activity 3423 times for $N = 32$ baboons, and 3112 times for $N = 57$ baboons (in R version 2.7.0, R Development Core Team, Vienna, Austria), which was equivalent to number of scan observations conducted for these two group sizes, and calculated B_s for each simulated data point for both the small group and the large group. The differences between the observed and simulated distributions were then compared with a Levene's test.

To assess the variables influencing behavioural synchrony within baboon groups, we used a beta-binomial generalized linear mixed model (GLMM) with logit link function (Rasbash et al. 2003). Scan data were collected repeatedly within and across days, and so 'scan number' and 'observation day' were fitted as nested random effects, to control for nonindependence of observations, that is, where synchrony at time t will influence the probability of synchrony at $t + 1$ or -1 . We fitted vegetation (open, grass, shrub, tree) and group identity (large, small) as categorical fixed effects. We fitted the proportion of females in the same reproductive state (four variables, one for each state), the diversity of female reproductive state (calculated in the same manner as B_s), group cohesion and the number of individuals in view during the scan as continuous variables. Entering the number of individuals in view as a continuous variable was required to test and control for its potential effect on group synchrony (e.g. synchrony might appear higher when fewer animals are in view, because a smaller number of animals may show a narrower range of activities). Group cohesion was log transformed to normalize data, and all continuous variables were entered with their mean as the reference point, for example mean group cohesion was set to zero, for comparison.

All fixed effects were entered and dropped sequentially until only those that explained significant variation remained: the minimal model. Each dropped term was then put back into the model to obtain its level of nonsignificance, and to check that significant terms had not been wrongly excluded. In all cases the same minimal model was derived by removing terms from the maximal model and adding terms to the simplest model. The continuous fixed effects were found to be statistically independent from one another (Pearson correlations: $P > 0.05$ in all cases), and so were initially entered into the models together. The diversity of

female reproductive state was entered into the model without the other variables of female state of which it is a composite. Biologically relevant two-way interactions and nonlinear effects were also tested, and are presented where found to be significant. Significance was tested using the Wald statistic, evaluated against the chi-square distribution.

RESULTS

We found that variability in behavioural synchrony was significantly larger than that predicted by a simple statistical model where individual baboons behave independently of one another (Levene's $\text{test}_{\text{smallgroup}} = 4722$, $N = 3422$, $P < 0.001$; Levene's $\text{test}_{\text{largegroup}} = 8626$, $N = 3122$, $P < 0.001$). We then proceeded to investigate what factors might account for the observed patterns of behavioural synchrony across individuals, using a GLMM.

First, we investigated and controlled for the proportion of individuals in view. As expected, the probability of behavioural synchrony was greatest when a smaller proportion of the group was in view. However, this effect seemed to be apparent only at relatively low numbers (<25% of group visible). In contrast, the differences in synchrony observed between intermediate and higher proportions of individuals in view were relatively small (Fig. 1).

An increased number of females in the same reproductive state were predicted to increase behavioural synchrony (prediction 1.1). This prediction was supported only in part. We found that the proportion of females in a pregnant state increased synchrony, but that the proportion of fertile females decreased synchrony (Table 1). No effect was found for other female reproductive states (lactating or nonfertile phase cycling females). Entering a measure of overall convergence in female state also had no effect (diversity of female states, Table 1). The numbers of pregnant and sexually swollen females thus appeared to act in opposite and opposing directions with respect to group activity synchrony. Behavioural

Table 1

Factors affecting the synchrony of activities within baboon groups as predicted from a GLMM analysis based upon 6535 scan observations of two groups

	Estimate	SE	Wald	P
Minimal model				
Hour of day	−0.04	0.01	25.41	<0.001
Proportion fertile females	−1.14	0.52	4.86	0.027
Proportion pregnant females	2.00	0.69	8.42	0.003
Habitat			48.25	<0.001
Desert 'open'	0.00	0.00		
Desert 'grass'	0.21	0.08		
Woodland 'shrub'	0.36	0.11		
Woodland 'tree'	0.55	0.08		
Group cohesion	−0.92	0.25	14.13	<0.001
Group cohesion ²	0.13	0.06	4.70	0.035
Proportion individuals in view	−3.65	0.55	44.31	<0.001
Proportion individuals in view ²	2.88	0.61	22.45	<0.001
Nonsignificant terms				
Group size			0.17	0.680
Small	0.00	0.00		
Large	0.08	0.08		
Proportion lactating females	−1.61	1.50	0.01	0.916
Proportion nonfertile females	0.16	1.49	0.01	0.913
Overall synchrony in female state	−0.12	0.38	0.10	0.749
Constant	3.03	0.30		
Observation day (random effect)	0.00	0.00		
Scan within day (random effect)	0.04	0.02		

The model was run with a beta-binomial error structure and logit link function, controlling for repeated observations within and across days (entered as random effects). The table shows parameter estimates (Estimate), standard errors (SE), associated test statistic (Wald statistic) and *P* values. Values for nonsignificant terms were obtained from fitting terms individually to the minimal model. Interactions were tested, but were not significant.

synchrony also decreased as a function of time of day, in support of prediction 1.2 (Table 1).

In the case of habitat effects, the baboon groups showed clear and significant differences in their synchrony between different vegetation types in line with predictions 2.1 and 2.2. Synchrony was highest among trees and lowest in open areas. Groups showed an intermediate level of synchrony in grass and shrub vegetation (Table 1, Fig. 2a).

In the case of group properties, where group cohesion was higher (high cohesion indicates individuals were spread over a smaller area), group behavioural synchrony also increased, in support of prediction 3.1. However, this was not a linear effect (Table 1). Where group cohesion was higher than average, the magnitude of this effect on synchrony was seen to be greatest (Fig. 2b). No overall difference was found between the large and small groups with respect to synchrony, failing to support prediction 3.2 (Table 1).

DISCUSSION

Two animals can either behave in the same way or not. The random expectation for the same behaviour to occur simultaneously in both is simply the product of the relative behavioural frequencies and durations in the two partners (Lamprecht 1985). But if there are more than two individuals in a group, it is more difficult to define behavioural synchrony (Engel & Lamprecht 1997). An animal may, at any point, behave in synchrony with some of its groupmates, but asynchronously with the others. One approach to this problem has been to assess the degree of synchrony of a specific individual with respect to its groupmates (Engel & Lamprecht 1997). A complementary approach, which we have developed in this study, has been to investigate the overall behavioural synchrony across all group members (see also

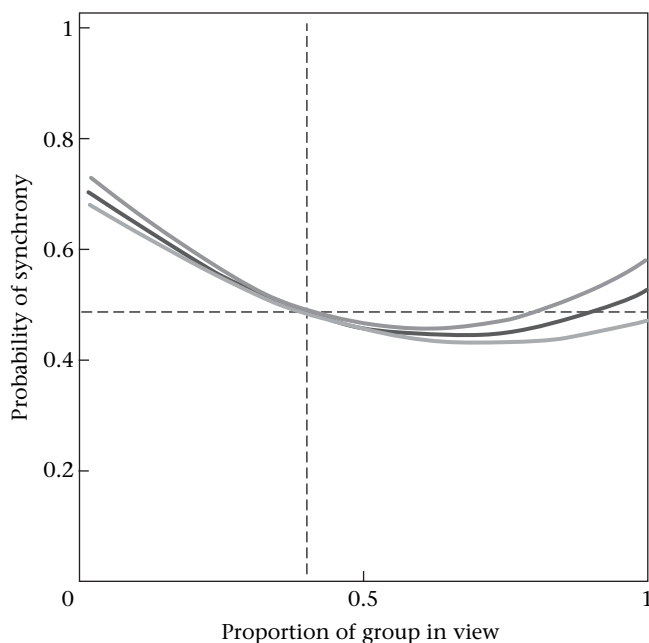


Figure 1. The effects of the number of baboons in view on the probability of group synchrony, as predicted from a GLMM controlling for repeated observations within and across days, and with all other significant effects set to their reference category/average value. The effect shown is relative to an average proportion of group members in view (approximately $N = 12$ and 24 individuals in the small and large group, respectively), indicated by the dashed axes. Predicted SEs are indicated by grey lines.

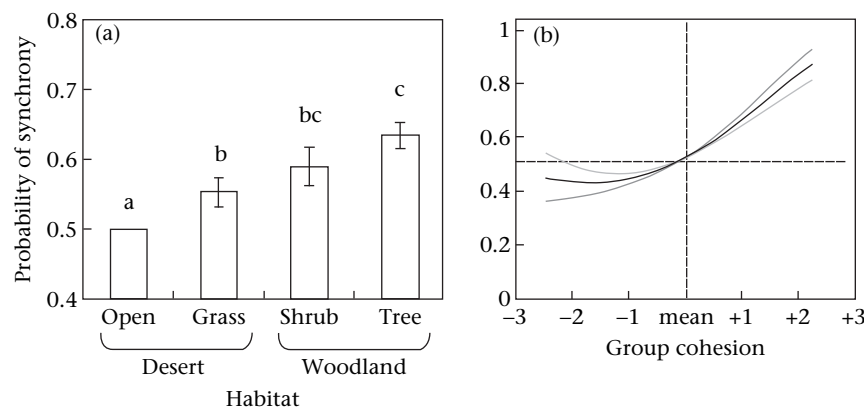


Figure 2. (a) The mean effect \pm SE of habitat categories upon synchrony. Significant differences between habitat types are indicated by different letters; where means do not differ, they share the same letter. (b) The effect of group cohesion on group synchrony. The effect shown is relative to average group cohesion (approximately an area of 80 m² per baboon), indicated by the dashed lines through the figure centre. SEs are indicated by grey lines. All results are predicted from a GLMM controlling for repeated observations within and across days, and with all other significant effects set to their reference category/average value.

Ruckstuhl 1999). We found that behavioural synchrony in two baboon groups differed from a simple statistical model in which all individuals behaved independently from one another, and tested three hypotheses relating to the activity-, habitat- and group-related processes that might be responsible for the observed patterns of synchronization.

Our results provide support for the activity-budgets hypothesis (H1), but are not entirely consistent with our initial predictions. We found that behavioural synchrony increased with the proportion of pregnant females, and decreased with the proportion of sexually swollen females. The former pattern was predicted on the basis that females in the same reproductive state share similar energetic requirements and are thus more likely to synchronize their activities (prediction 1.1). However, the proportion of females in other reproductive states (and also overall concurrence in state) should have also had a positive influence on synchrony if this were the case, which they did not. How can this inconsistency, and the significant negative effect of the number of sexually swollen females, be resolved? One possibility is that these emergent patterns arise from a combination of higher energy requirements in certain female states and a disruptive influence on male behaviour in others. On the one hand, pregnant females have higher energetic requirements that increase their foraging time (and consequently reduce time engaged in other activities) and may thus increase group synchrony. On the other hand, copulations and mate guarding with fertile females could disrupt male behaviour (Alberts et al. 1996) and reduce group synchrony. This leaves the lactating and nonfertile female categories, whose numbers did not have a significant effect on group synchrony. In the case of nonfertile females, there may be no influence on synchrony because neither energy nor male effects are present. In the case of lactating females, male–female ‘friendships’ in response to the threats presented by infanticidal males (Lemasson et al. 2008), together with female strategies for coping with energetic costs of lactation at different infant ages (Barrett et al. 2006), may act to increase and decrease synchrony respectively, resulting in no overall effect.

In support of the second prediction of the activity-budgets hypothesis, we found that behavioural synchrony was highest in the morning and decreased throughout the day. We suggest that early in the day when all individuals are hungry and need to forage, synchrony in behaviour is more likely to occur as a consequence of many individuals foraging and travelling together between food patches. In contrast, later in the day, as individuals become satiated

at different rates as a consequence of stochastic processes and phenotypic variation, activity patterns diverge and synchrony declines. Stochastic processes refer to the role that chance plays in the number and quality of food patches an individual encounters over the course of a day. Phenotypic variation refers to a variety of possible factors that may influence satiation rates. One of these is body size variation: younger animals have lower food requirements, owing to their smaller size, and thus will stop foraging before older (larger) animals. Feeding competition may be important too. Low-ranked individuals can be excluded from prime feeding areas resulting in these individuals having to engage in other activities (e.g. searching for food elsewhere), which in some species can ultimately lead to groups breaking up with subordinates foraging alone (e.g. green woodhoopoe, *Phoeniculus purpureus*: Radford & Du Plessis 2003). Given that dominant baboons often exclude subordinates from monopolizable food patches, but that groups only rarely fission (King et al. 2008), subordinates might need to increase their foraging time later in the day, once dominants are satiated. This would result in lower behavioural synchrony at the group level. Note also that this would not necessarily require individuals of different rank to vary their time spent feeding (Barton & Whiten 1993), but only that they feed at different times.

Concerning the habitat-constraints hypothesis, we found that behavioural synchronization was highest in woodland habitat and lowest in desert habitat, as predicted by both food patch configuration and predation risk (predictions 2.1 and 2.2). However, disentangling the effects of foraging and predation risk on group synchrony is difficult. One possible approach is to consider the interaction effects. If predation were important, we might expect the smaller group to be more synchronous in high-risk woodland habitat than the larger group. However, no such interaction between group and habitat was detected, suggesting that foraging effects may be more important. This is further supported by a complementary study investigating social foraging in these baboon groups. King et al. (2009) showed that in woodland habitat ‘scrounging’ behaviour was more frequent: individuals were less likely to search for food themselves, but instead joined the food discoveries of others. This will act to increase the number of individuals foraging within food patches at any time. Nevertheless, further work using a spatially explicit analysis of synchrony with respect to distance from refuges would help to separate further these relative effects on behavioural synchrony.

We have also shown that the spatial properties of baboon groups (hypothesis H3) can have an effect on behavioural

synchrony: specifically, that synchrony increases with group cohesion. Given that group members may actively coordinate their synchronous behaviour at least some of the time, and that such coordination is likely to be facilitated by the monitoring of their groupmates, this finding is consistent with the idea that the acquisition of social information is mediated by neighbour distance (Pitcher & Parrish 1993; Fernandez-Juricic & Kacelnik 2004; Fernandez-Juricic et al. 2007). The nonlinear nature of this relationship further suggests that there is a certain neighbour distance beyond which monitoring and synchrony become very difficult, but below which they become progressively easier as proximity increases. However, this pattern may also result from the constraints certain behaviours place on cohesion. Specifically, when groups are resting, they tend to cluster together and groom one another (which in itself requires at least two individuals to be in close proximity), which would generate an apparent relationship between cohesion and synchrony. To investigate the potential for such confounding effects, further investigations into behavioural synchrony at a finer scale are required, not least to elucidate the causal direction in our synchrony–cohesion finding (i.e. synchrony causing cohesion or cohesion facilitating synchrony). Further research is also required to explore potential group size effects (prediction 3.2): we found no evidence for such a pattern, but our small sample size makes this a preliminary analysis only.

Overall, we have shown that the achievement of behavioural synchronization (measured as diversity in activities among group members) can be affected by variation in activity budgets across individuals, a result that is consistent with previous research on ungulates (e.g. Ruckstuhl 1999; Ruckstuhl & Kokko 2002; Michelena et al. 2006). Furthermore, we have highlighted the effect of habitat constraints and group properties on patterns of synchrony, which have to date received relatively less attention in the literature. Given the simplicity of our approach, requiring only simple activity budget data complemented by observations of the social and ecological environment, there is enormous scope for testing the relative importance of activity budgets, habitat and group properties on behavioural synchrony across different populations and species.

Adopting such a comparative approach may also allow us to uncover the mechanisms through which synchrony might be mediated. There are two possibilities. Synchrony may be triggered either by environmental processes, where shared environmental conditions stimulate individuals to adopt similar behaviours to their neighbours independently (Engel & Lamprecht 1997) or by social processes. Although our finding of habitat-associated synchrony suggests an influence of environmental mechanisms, the group cohesion effect indicates that social mechanisms also play a role. In the latter case, self-organization theory suggests that behavioural synchrony can arise from relatively simple interaction patterns among group members (Sumpter 2006), since multiple individuals following simple local movement rules can produce extremely synchronous behaviour (Couzin & Krause 2003). Such mechanisms are appealing because they suggest that behavioural synchrony can be explained without invoking complex decision-making abilities at the level of the individual (Couzin 2007). However, self-organizing processes work best where individuals share the same goal, for example eusocial insects choosing a new nest site (Lindauer 1957; Visscher 2007) or navigating birds migrating to a specific location (Guilford & Chappell 1996; Simons 2004). In baboons, and many other social taxa, there are conflicts of interest (Conradt & Roper 2000), and individuals can communicate globally as well as locally with all other group members (e.g. Boinski 1993). In these cases, activity synchrony may be determined by the average preference of all group members (Conradt & Roper 2003). Recent research further suggests that specific

individuals may precipitate shifts in the activity of entire groups and coordinate their behaviour (King & Cowlishaw 2009b; King et al. 2009, in press; Lusseau & Conradt 2009).

In the future it is hoped that we will be able to elucidate the links between such complex social interactions with the emergent patterns of synchrony of the kind described here, to produce a more complete understanding of the phenomenon of behavioural synchrony in group-living animals.

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