Behavioral sequences across multiple animal species in the wild share common structural features

Pranav Minasandra*[a,b,c,d], Emily M Grout[a,b,c,d,e], Margaret C Crofoot[a,b,d,e], Vlad Demartsev[a,b,d,f], Andrew S Gersick[g], Ben T Hirsch[e,h], Kay E Holekamp[i,j], Lily Johnson-Ulrich[f,k], Amlan Nayak[a,b,l], Josué Ortega[a,e], Marie A Roch[m], Eli D Strauss[a,b,d], and Ariana Strandburg-Peshkin[a,b,d,f]

[a]*Department for the Ecology of Animal Societies, Max Planck Institute of Animal Behavior, Konstanz, Germany;* [b]*Department of Biology, University of Konstanz, Konstanz, Germany;* [c]*International Max Planck Research School for Organismal Biology, Konstanz, Germany;* [d]*Centre for the Advanced Study of Collective Behaviour, University of Konstanz, Konstanz, Germany;* [e]*Smithsonian Tropical Research Institute, Panama;* [f]*Kalahari Meerkat Project, Kuruman River Reserve, Northern Cape, South Africa;* [g]*Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ, USA;* [h]*Division of Tropical Environments and Societies, James Cook University, Townsville, Australia;* [i]*Department of Integrative Biology, Michigan State University, East Lansing, MI, USA;* [j]*Program in Ecology, Evolution, and Behavior at Michigan State University, East Lansing, MI, USA;* [k]*Department of Evolutionary Biology and Environmental Studies, University of Zurich, Zurich, Switzerland;* [l]*Indian Institute of Science, Education, and Research, Mohali, India;* [m]*Department of Computer Science, San Diego State University, San Diego, CA, USA*

Abstract

Animal behavior can be decomposed into a continuous sequence of discrete activity bouts over time. Analyzing the statistical structure of such behavioral sequences provides insights into the drivers of behavioral decisions in animals. Laboratory studies, predominantly in invertebrates, have suggested that behavioral sequences are characterized by multiple timescales and exhibit long-range memory, but the extent to which these results can be generalized to other taxa and to animals living in natural settings remains unclear. By analyzing accelerometer-inferred predictions of behavioral states in three species of social mammals (meerkats, white-nosed coatis, and spotted hyenas) in the wild, we discovered surprisingly consistent structuring of behavioral sequences across all behavioral states, all individuals and all study species. Behavioral bouts were characterized by decreasing hazard functions, wherein the longer a behavioral bout had progressed, the less likely it was to end within the next instant. The distributions of bout durations were also heavy-tailed (typically power-law or truncated power-law), suggesting that bouts of behavior cannot be characterized by a 'typical' duration for any of the behaviors we studied. Finally, the predictability of an animal's future behavioral state as a function of its present state always decreased as a truncated power law for predictions made farther into the future, with very similar estimates for the power law exponent across all three species. These patterns suggest similar structural principles in behavioral sequences across all study species. Why such shared patterns emerge remains unknown. We explore multiple plausible explanations, including environmental non-stationarity, behavioral self-reinforcement via positive feedback, or a combination of multiple relevant timescales driven by the hierarchical nature of behavior. The existence of highly consistent patterns in behavioral sequences across all three study species suggests that these phenomena could be widespread in nature, and points to the existence of fundamental properties of behavioral dynamics that could drive such convergent patterns.

Keywords—behavioral dynamics, bout duration distribution, survival analysis, accelerometer, meerkat, white-nosed coati, spotted hyena

Significance statement

The study of animal behavior seeks to understand how and why animals do what they do. This pursuit of general principles governing behavior across species can be approached by first understanding *when* animals choose to change their behavioral states (e.g., switching from walking to standing, or to running). Using accelerometer-inferred behaviors of three social mammals, we uncover common structural patterns in their sequences of behavior. We explore two explanations, involving either positive feedbacks or the interaction of several independent time-scales, about how such common patterns arise.

1 Introduction

A day in the life of an animal consists of a series of transitions between discrete behavioral states – for

*pminasandra@ab.mpg.de

example, a meerkat might wake up, stand in the sun outside its burrow as the air temperature rises, then eventually move off in search of food, occasionally scanning the skies for predators. When combined, these actions describe a behavioral sequence. The behavior of all organisms, from oomycetes to orcas, consists of such behavioral sequences, and these sequences in turn reflect complex processes in the animal brain that, together with environmental information, underlie decisions about which behavior to perform at any moment in time [1]. Characterizing the statistical properties of behavioral sequences and, in particular, quantifying the time-scales that structure them [e.g., 2, 3], can shed light on the underlying decision-making processes that generate observed patterns of behavior.

It is likely that some aspects of these decision-making processes are shared across species, either because of common evolutionary origins or convergent evolution. Searching for common patterns in the statistical structure of behavioral sequences is therefore a powerful tool for identifying potential general principles of animal behavior.

Several previous studies have pointed towards the existence of a large number of operant timescales in the organization of behavior [2, 4–8], such that behavior acts as a process with long-range memory. Taken together, work on different species suggests the potential for general, widespread structural principles in behavioral sequences, but no studies have yet applied these analytical approaches to empirical data on multiple types of behavior in multiple species in natural settings to directly assess the shared structural features (if any) of behavioral sequences.

Here, we use continuous accelerometer data recorded via tracking collars to infer behavioral sequences across three species of social mammals – 15 meerkats (*Suricata suricatta*; small burrow-living mongooses), 9 white-nosed coatis (*Nasua narica*; fruit-eating omnivores), and 5 spotted hyenas (*Crocuta crocuta*; large carnivores). Applying three analytical approaches to analyze data from each species, we find shared structural properties across all species, behaviors, and individuals, indicating common features in the underlying decision-making processes at play. We hypothesize that such common decision-making processes might be the result of equally common drivers of behavior: non-stationarity due to animals responding to constantly-varying external variables, or a multiplicative decision-making structure as a feature of behavioral algorithms.

1.1 Characterizing behavioral sequences

There are many ways to characterize a behavioral sequence. Here we focus on three approaches: measuring hazard functions, characterizing bout duration distributions, and quantifying the decay of mutual information between present and future behavioral states. These three methods provide complementary perspectives on the dynamical structure of behavior.

Behavioral hazard functions

A bout is a process that has a defined start and end time. In the case of behavior, a bout defines a contiguous period of time during which an animal performs the same behavior, for example walking, resting, or foraging. Survival analytic concepts [9, 10] are useful in understanding the nature of processes with observable beginnings and ends. Of these concepts, specifically useful is the hazard function, $h(t)$, which quantifies the instantaneous probability of a process (in this case a behavior) ending given that it has already been in progress for time t. I.e., if τ is the survival time of a behavioral bout from start to end, then

$$h(t) = \lim_{\epsilon \to 0} \frac{1}{\epsilon} \Pr(t \leq \tau < t + \epsilon \mid t \leq \tau).$$

Qualitatively, an increasing hazard function represents a process that is wearing out, becoming more likely to end as time passes [e.g., the survival of leukemia patients, 11]. Conversely, a decreasing hazard function represents a process that is reinforced, becoming progressively less likely to end as time passes, such as the survival of patients recovering from surgeries [11] or the operational durations of spacecraft [12]. Constant (i.e., flat) hazard rates are associated with memory-less processes, such as the radioactive decay of an unstable atomic nucleus. Many commonly used models of behavior and movement, such as simple Markov models, assume memory-less processes, where individuals switch between behaviors with constant transition probabilities dependent only on their current state. Such Markovian assumptions are often made for the sake of analytical tractability despite the fact that animal behavior is often non-Markovian [13].

The shapes of hazard functions can give information about the underlying behavioral processes. For instance, if the hazard function for a particular behavior was found to decrease up to some time T and then increase after that, we might predict that this timescale T is important to the animal's decision-making process. The shape of the hazard function can provide insights into the nature of memory in the behavioral sequence—for instance, decreasing hazard functions might link to self-reinforcing processes that have strong long-range order [14].

A priori, we expect different behaviors to show bouts characterized by different types of hazard

functions. For instance, behaviors that are energetically expensive or risky might have bouts with increasing hazard rates, since the animal becomes progressively less likely to continue such behaviors the longer they have persisted. Conversely, behaviors with increasing returns, such as extractive foraging from a complex food resource (such as a carcass or fruit with a tough exterior [15], or a termite mound [16]) that progressively yields higher quality nutrition as the animal forages, might be expected to have decreasing hazard rates up to the point where returns start to diminish. Since situations of diminishing marginal returns are likely to be more common in nature than those with increasing returns, we might expect that hazard functions should most often increase as the individual engages in the behavior to accomplish a certain task or meet a certain need; and therefore becomes more likely to switch to the next state as time progresses. This seems to be a common expectation. For instance, Gygax et al [10] write about sleep bouts: "this likeliness [i.e., the hazard function] may increase the longer the animal has been in the state".

Behavioral bout duration distributions

Hazard functions of processes are linked directly to the distributions of process survival times (here, the durations of bouts of each behavior), such that knowing one provides information about the other. The durations of behavioral bouts are sometimes heavy-tailed (see references below). 'Heavy-tail' refers to a tail (the part of the distribution associated with large values, e.g., long bouts) which decays slower than an exponential distribution. Heavy-tailed distributions are characterized by an unusually high occurrence of very large values. Some examples of heavy-tailed distributions are the log-normal, stretched exponential, power-law, and truncated power-law distributions, of which the latter two are of special interest. If a variable is normally distributed, then a typical value, such as the mean, can convey useful information about the distribution of this variable. For example, if the time an animal spends in a given bout of vigilance were normally distributed with a mean of 10 seconds, it would imply that the timescale of 10 seconds is behaviorally relevant for that animal – perhaps a typical scan of the environment takes 10 seconds to complete. Because power-law and truncated power-law distributions show very high or infinite variances and means [17], they are difficult to characterize with such single 'typical' values. In the case of behavioral bouts, a heavy-tailed distribution would imply that it is difficult to choose a single time scale at which behavioral decisions can be presumed to occur. Such *scale invariance* is associated with power-law bout duration distributions. Penguin [18] and macaque [19] foraging patterns as well as *Drosophila* flight sequences [20] and activity patterns [21] show scale invariance. Moreover, power-law distributed step lengths have been reported in movement trajectories of numerous species [the Lévy Flight Foraging Hypothesis, 22, 23], which indicate a power-law bout duration distribution for movement states.

Power-law and truncated power-law distributions are of interest in studies of complex systems, often indicating common patterns in their underlying structures. [17, 24]. A power-law distributed variable τ has a probability density $f_\tau(t) \propto t^{-\alpha}$. Power-law distributions can have very large population means and variances (sometimes infinite, when $\alpha < 2$ and 3 respectively), and always show decreasing hazard functions [25]. Truncated power-laws show power-law properties up to some cutoff, beyond which they behave similarly to exponential distributions ($f_\tau(t) \propto t^{-\alpha}e^{-\lambda t}$). Heavy-tailed distributions are often associated with phenomena with memory and positive feedback (e.g. self-reinforcement): the distributions of wait-times between certain events is often power-law distributed: e.g., the duration between earthquakes [26], neuronal avalanches [27], armed human conflict [28], or between consecutive e-mails [29]. Such events typically occur where some variable slowly needs to grow (e.g., pressure, stress, energy, or motivation) in the wait-time until the event is suddenly precipitated [30]. Bouts of inactive human behaviors (e.g., waiting for an event to occur) are theorized to be power-law distrubuted [29], and power-law distributions are empirically found in resting human patients [31–33]. Furthermore, similar results are seen in other species such as mice [31].

Mutual information decay over time

Beyond analyzing the structure of behavioral bouts, an information theoretic perspective can also reveal the timescales over which behavioral sequences show memory. Predictivity measures the extent to which knowledge of the animal's current behavioral state is predictive of its future state (conversely, the extent to which an animal's past behavior influences its current state). The predictive value of the current state decays as one moves forward in time (i.e., it is increasingly difficult to forecast behavior further into the future). The scale at which predictivity decays can help us quantify long-range memory in the animal's behavioral sequence. A scale invariant (power-law) decay would indicate complex, multi-level processes [34] that together generate behavior such that an animal's present state is informative very far into the future. Quantifying the rate at which the future's dependence on the present state decays in an animal's behavioral sequence can thus be informative about underlying decision-making processes. For instance, ex-

periments on *Drosophila* have revealed long-term order in the fruit-flies' behavioral sequences, interpreted as the result of behavioral processes acting at multiple time scales [2, 13, 35].

2 Results

Deploying accelerometers on individuals of three species, we used either conventional or machine-learning based methods to quantify individuals' behavioral sequences. Based on feasibility, behavioral sequences were generated at varying levels of precision while distinguishing different behaviors—coati behavioral sequences were composed of high vs low activity, whereas hyena and meerkat behaviors were more precisely identifiable, so that their sequences were composed of categories of kinematic states such as standing, walking, vigilance, and foraging (see Methods).

2.1 Decreasing hazard functions in bouts of all behaviors

From each individual's sequence, we extracted the durations of all bouts of each behavioral state. From these durations, we quantified the hazard function for bouts of each behavior.

In contrast to our *a priori* expectations, we found that hazard functions were always decreasing, across all behavioral states, all individuals, and all species (Figure 1). This result implies that the longer an animal has been in a given behavioral state, the less likely it is to switch to a new state within the next instant.

2.2 Heavy-tailed bout duration distributions for all behaviors

Several bout duration distributions can lead to decreasing hazard functions. To more fully characterize the variability in bout durations, we quantified bout duration distributions for all behavioral states across all three species, and for each individual separately.

We found that bout duration distributions for a given behavioral state were remarkably consistent across individuals, and were most often heavy-tailed (SI Table S2 and Figure 2), with almost all individuals showing power-law or truncated-power-law bout duration distributions across all behavioral states. Estimates of the power-law exponent, α, were almost always between 1 and 3, signifying an infinite population variance, and sometimes, an infinite population mean of bout durations. For a given behavior, all individuals usually showed bout duration distributions with very similar parameter values. The finding of heavy-tailed bout duration distributions implies that it is difficult to identify a 'typical' time-scale for behavioral bouts for any of the behaviors quantified here.

2.3 Long term predictivity of behavioral sequences

To quantify memory in the behavioral algorithms, we asked how long into the future the current behavior of an animal remains predictive. To quantify this *predictivity*, for each individual, we computed the adjusted mutual information [36] between its behavioral state at time t and time $t + \tau$.

In all three species, we found that the mutual information between behavioral states decays over time τ as an exponentially truncated power-law (Figure 3), with a surprisingly conserved power-law exponent (meerkats: 0.193 ± 0.05, coatis: 0.158 ± 0.014, hyenas: 0.187 ± 0.014; all variation here is that measured across individuals, SI Table S3 A-C). Interestingly, these exponents are also strikingly similar to the scaling dimension found recently in *Drosophila* behavioral sequences [35, 0.180 ± 0.005]. The timescale of truncation (i.e. the transition from power law to exponential decay) was consistent across all individuals within a species: at $\sim$ 1000 s (or $\sim$ 15 minutes) in all meerkats and coatis and $\sim$ 3000 s ($\sim$ 45 min) in all hyenas.

As a separate way to quantify long-range memory in behavior over time, we also performed Detrended Fluctuation Analyses (DFAs, which quantify long-range memory or 'dependence' in time series) [37] for binary sequences of each behavior [as in 6, 19, 38]. We found that the exponent α_{DFA} was around 1.0 for all behaviors, individuals, and species in our study (see SI Appendix, Table S4 A-C), which also indicates long-range memory in these behavioral sequences.

2.4 Effect of imperfect classification

Errors in the recognition of behaviors can split long bouts into two or more shorter bouts so that even small error rates in behavior identification can have complex, non-trivial effects on the bouts quantified from their output. This effect leads to the shortening of longer bouts with a high probability, which may lead to false negatives in the quantification of heavy tails. Using simulated behavioral sequences and classifiers with error rates we could specify (see SI Appendix Text 'Simulating the effect of classifier error on the quantification of bout duration distributions', Figure S3A), we found that classifier error indeed produces biases against the detection of heavy tails in bout duration distributions, such that the most error-prone classifiers never detect a heavy tail. Unexpectedly, we also found that, at a particular error range (≈ 0.3), classified behavior sequences were characterized erroneously, almost always as truncated power-law distributions of bout durations (Figure S3B). This spurious detection of heavy tails most likely emerges through the preferential destruction of longer bouts as compared to shorter ones (Figure S3C). Since the longest bouts

in our data last up to 10^4 seconds (3 hours), for error-prone classification to explain our empirical findings, animals would need to exhibit a 'true' bout duration distribution with bout lengths two orders of magnitude greater than the longest ones observed in our data (as in Figure S3C), or around 10^6 seconds (11 days) long. The existence of such long bouts seems exceedingly unlikely, making it highly improbable that classifier error can explain our broad findings of heavy-tailed distributions. We nevertheless suggest that future studies investigating the effects of classifier error on behavioral sequence analysis would be important to shed more light on this general issue.

3 Discussion

Taken together, our findings highlight common patterns in the organization of behavioral sequences across behaviors, across individuals, and across species. We found power-law and truncated power-law distributions of behavioral bout durations, suggesting a scale-free organization of behavior, with most behaviors not being characterized by a single 'typical' timescale. As bout durations of some behaviors followed truncated power-law distributions, our results suggest that this scale invariance typically only applies until some large time scale, beyond which the dynamics are largely memoryless. We also found a similar truncated power-law decay in the predictivity of an animal's present state of its future state, indicating that these behavioral sequences are characterized by long-range memory at least up to some timescale (here roughly 15 minutes for meerkats and coatis, and 45 minutes for hyenas).

Our analyses simplify the behavior of an animal, so that all our behavioral sequences are composed of coarse behavioral labels, and the level of coarseness and temporal resolution are different among study species. Such simplification is useful as it provides great analytical tractability while still retaining temporal patterns of behavioral structure. Still, we note that behavior sequences like these do not describe behavior in its full complexity in an animal, due to which care needs to be taken in inferring and understanding our results. For instance, courtship behavior in a male hyena would form behavioral sequences with short bouts of walking towards and away from a female. That these bouts arise during courtship would tell us a lot about the dynamics of the bouts of movement at this time. Reducing complex behaviors to sequences of simple kinematic behavioral states necessarily loses such contextual information, yet this reduction in complexity also enables a broader perspective on behavioral sequences in general, as we have done here.

The existence of shared structural properties in behavioral sequences suggests that these patterns may be driven by common underlying mechanisms. While these mechanisms remain unknown, we propose here two possible explanations that could give rise to such consistent, widespread patterns. First, positive feedback processes may be a general feature of animals' behavioral algorithms. Second, the interaction of environmental and/or physiological processes across timescales may introduce memory into behavioral processes that are themselves memory-less.

3.1 Behavioral algorithms may contain positive feedback motifs

Our discovery of decreasing hazard functions—where long bouts of behavior tend to get longer—across all behaviors, individuals, and states points towards the possible existence of positive feedback mechanisms in behavioral algorithms. While positive feedback is a common feature in the organization of neural circuits [39–41], these positive feedback mechanisms do not necessarily need to be neurological. Since all three species we investigated here are social, one possible explanation for the convergent patterns is social feedback, where individuals socially reinforce each other's behavior resulting in prolongation of behavioral bouts. Using simulations of interacting memory-less animals (see SI Appendix, Text 'Simulating individuals who socially reinforce their behaviors', Figure S4), we show that such social reinforcement can in principle lead to decreasing hazard rates as observed in our data.

This argument raises the possibility that behavior is broadly governed by positive feedback mechanisms. These positive feedbacks could operate at the level of internal dynamics, social feedback , environmental feedbacks, or a combination of these factors. Such positive feedback mechanisms could also cause the scale invariance of behavioral sequences, as power-law distributions are associated with positive feedbacks [42, 43]. This scale invariance might then break down at longer timescales due to environmental changes occurring at a somewhat slower timescale (e.g., change in time of day, or change in type of habitat as the animal moves), leading to the observed exponential truncations of bout duration distributions seen in many behaviors.

Our finding of power-law and truncated power-law bout duration distributions also raises the interesting possibility that behavioral algorithms act, at least in part, in a 'multiplicative' instead of 'additive' sense. That is, similar to how an exponential distribution of bout durations arises from a constant hazard rate, it can be shown mathematically that power law bout duration distributions are linked to processes that show a constant doubling probability [25, and SI Appendix, Text 'Doubling probability in random variables']. In other words,

the probability that a bout which has gone on for time t continues until time ηt remains constant with t (where $\eta > 1$ is any multiplicative factor). When applied to behavioral bouts, such a structure could therefore indicate that decisions about whether to change behavior do not act instant-to-instant, but rather the constant element of decision making instead governs whether the animal should occupy the current behavioral state η times longer than it already has. For instance, if a meerkat has been foraging for one minute, the probability that it continues foraging for another one minute interval will be the same probability as the probability that it continues for another ten minutes after having already foraged continuously for ten minutes. Mechanistically, such dynamics could come about if the decision to change behaviors or not is made less and less frequently the longer an animal has been performing a behavior. Similar arguments have been made before in the context of movement decisions to explain Lèvy Flights [44].

The argument that behavioral decision-making is inherently characterized by positive feedbacks or multiplicative structure has the advantage of being the most straightforward interpretation of our results, in that it attributes the observed patterns directly to the underlying behavioral algorithms at play. However, this argument is difficult to prove or disprove based on behavioral data alone. Future studies which also monitor brain activity might help detect candidate positive feedback motifs in the brain, and shed some light on the validity of this explanation.

3.2 Behavioral algorithms may be driven by processes acting at different time-scales

Decreasing hazard functions and apparently scale invariant dynamics could also come about as a result of the interaction of several individually memory-less processes, each acting at a different time-scale [5, 34, 45, 46]. Such a combination of processes could arise from different mechanisms, described below.

First, we note that not all mixtures of memory-less processes generate heavy tails. Simulating pairs of exponential distributions with randomly assigned parameter values, we found that of 50,000 simulations, none were classified as power-law or truncated power-laws using our fitting methods (SI Appendix 'Simulating random exponential distribution mixtures to quantify spurious heavy-tails'), implying that our results are not easily produced by simple mixtures-of-exponentials. Specific, more complex mixtures of a larger (potentially infinite, as in [46]) number of memory-less processes could adequately explain the heavy-tailed distributions observed in our data. Explanations following this line of arguments need to thus explain the similar structuring of mixtures of memory-less processes that generate identical bout duration distributions in all behavioral states across individuals and species.

It has long been argued that animal behavior is hierarchically organized [1, 2], and as such, is probably governed by processes operating at different time-scales at each level of this hierarchy [2, 7, 34, 47]. For example, an animal's behavior can be coarsely categorized into high and low activity levels. There are bound to be more behavioral states that are encompassed within each of those labels (e.g., standing, sitting, lying down are all low activity behaviors). The rates of state-switching between sub-states within each activity level are likely different from the rate of switching between activity levels. This hierarchy could arguably lead to the perception of prolonged bouts, e.g., of 'low activity', while the animal switches between the sub-states encompassed within that label.

Since we expect neither the animal nor the environment to remain the same through time, we expect the same behavior to occur in multiple contexts (e.g., a hyena could be walking in the context of foraging, mate finding, or returning to a den). Different memory-less processes associated with each of these contexts could be sufficient to explain our results, and connect well with the idea of hierarchically organized behavior with different time scales acting at each level [4]. If the animal's environment varies at a temporal scale slightly slower than the scale at which behavior occurs (which is likely to be true in all animals that move across heterogeneous landscapes), the idea of multiple contexts can be generalized to infinitely many contexts (one for each state of the environment). These contexts could be associated with different (otherwise memory-less) processes, leading to the emergence of power-laws in bout duration distributions via the combination of a large number of exponential processes. Such a mechanism has recently been theorized and mathematically formalized [45], and could also explain our results.

The observed prevalence of long time-scales and power-law relations in all species considered here can, in these ways, be attributed to multiple intersecting memory-less processes. At the same time, this explanation raises more questions—for instance, how is it that these interacting timescales always combine in such a way to produce apparent scale invariance, particularly with such similar parameter values? Quantifying behavior at multiple time scales requires better analytical approaches [2, 5, 34], as well as further empirical data to test what combinations of times scales may be operating. Further, since arbitrary interacting time scales do not produce the appearance of scale invariance, we need to ask what time scales apply to what con-

texts, specifically considering the hierarchical organization of behavior: i.e., what time scales apply at what levels of this hierarchy and why.

3.3 Possible fitness implications of behavioral sequence structure

The mechanisms hypothesized above do not necessarily imply any kind of adaptive origin. Nevertheless, the possible fitness implications of the structure of behavioral sequences merit consideration.

One aspect of behavioral sequence structure with clear fitness relevance is activity budgeting. Activity budgets are allocations of proportions of total time to different behavioral states [48–50]. The optimal allocation of an activity budget to various behaviors is likely to be driven by the costs and benefits associated with each behavior [51, 52]. Budgets can be adhered to in multiple ways. For instance, an animal may choose to engage in a specific behavior for a set period of time, or may break the behavior into multiple bouts in order to optimize multiple goals such as foraging and predator detection. Algorithms for producing optimal sequences of behavior are not known [but see 53, 54] and it may also be the case that animals use sequences that are 'good enough' to meet their needs. It is likely that the large variation that has been observed in bout durations in these data may be attributable to dynamic goals that affect the duration of an engaged behavior, and may somehow be of adaptive value. Future theoretical and empirical studies investigating time budgeting in terms of not only total time allocation but also how such allocations are divided could shed light on this topic.

Another phenomenon to which an adaptive value of scale invariance has been attributed is movement following Lèvy Flights, where step sizes during movement follow a power law distribution [22, 23]. The power-law distributed bouts of movement behaviors we find here accord with prior literature reporting Lévy Flights, however here we have also discovered power-law (or truncated power law) bout duration distributions across many behaviors – both those related to movement and those related to rest or inactivity. This raises the intriguing possibility that Levy flight-like patterns of movement, which have, heretofore, been hypothesized to arise as a consequence of optimal movement strategies [23, 55], could, alternatively, arise due to general patterns of behavioral dynamics that produce heavy tailed distributions of behavioral bouts [see also 56].

4 Conclusions

Analyzing behavioral sequences through three different approaches, we have found remarkable similarities in the dynamics of behavior across three species in the wild. We also found notable similarities across different behaviors in all three species, in contrast to our *a priori* expectations that our analyses should show qualitatively different results for different types of behaviors. These phenomena together strongly suggest that behavior in the wild across species is governed by algorithms with processes likely acting at various time-scales. We theorize that, at least in the species we have studied, these patterns could arise via social or ecological positive feedback mechanisms, via changing environmental conditions, or some combination of both. Independent of their mechanistic explanation, our results imply that decision making processes across our three study species share common structural properties. The surprising cross-species similarity of our results also raises the question of how widespread these phenomena are across the animal kingdom. Future studies quantifying behavioral sequences through biologging and other approaches can expand these analyses to a wide range of species in natural settings, with potential to shed light on general features of behavioral algorithms in animals.

5 Methods

5.1 Study species and primary data collection

Three species of group-living mammal were considered in this study. Multiple individuals from each species were fitted with collars containing several sensors including accelerometers, which were used to infer behaviors. In each case accelerometer readings were carried out over the course of several days (ranging from 2 - 47 depending on individual and species; see Table S1). In all cases, accelerometer readings were synchronized with GPS time. Here we give a brief description of each species and the data collection methods. Additional details can be found in SI Appendix, Text 'Primary data collection and behavioural classifier design'.

Meerkats (*Suricata suricatta*) are social mongooses native to arid parts of southern Africa. They live in highly cohesive groups with a despotic social organization [57]. Meerkats are opportunistic generalists that forage on small invertebrate and some vertebrate prey distributed across their desert habitat by digging in the ground [58]. At night, meerkat groups find shelter in communal burrows, underground structures typically consisting of multiple entrances linked by tunnels, that can persist over many years [59]. Data were collected from all members of three meerkat groups at the Kalahari Research Centre, Northern Cape, South Africa. These individuals wore custom built collars which recorded continuous accelerometery data. Accelerometer data were recorded throughout the day at 10 Hz in some groups, and at

50 Hz in others. Accelerometer resdings were synchronized with GPS (Axy-Trek Mini, Technosmart, Colleverde, Italy).

White-nosed coatis (*Nasua narica*) are diurnal members of the procyonid family [60]. Females live in groups with their offspring, whereas adult males are mostly solitary [60–63]. Coatis are omnivorous and spend the majority of the day foraging for leaf litter invertebrates and fruits [64]. Group living coatis groom and play with one another as well as sleep together in tree nests. Data were collected from all 10 members of a coati group in Soberania National Park, Panama. These individuals wore collars that recorded continuous tri-axial accelerometery data at 20 Hz for three hours every day (between 11:00 to 14:00 UTC, corresponding to 06:00 to 09:00 local time), synchronized to GPS data (e-Obs Digital Telemetry, Gruenwald, Germany). As continuous accelerometry was limited to three hours a day, we could not measure bouts longer than 3 hours, if any.

Spotted hyenas (*Crocuta crocuta*) are large social carnivores found throughout sub-Saharan Africa. Their bone-crushing jaws and efficient loping gait make them well-adapted for cursorial hunting and scavenging [65, 66]. They live in large, mixed-sex groups where all adults of both sexes are reproductively active and breed non-seasonally [67]. Hyena societies are structured by high degrees of fission-fusion dynamics, where despite living in large groups, they spend most of their time alone or in association with a few group-mates [68]. They are most often active at night and the hours around dawn and dusk, although they can be active at any time of day [69]. Data were collected from five female hyenas residing in the Talek clan in the Maasai Mara National Reserve in southwestern Kenya [70]. These individuals wore Tellus Medium collars (Followit, Sweden) fitted with custom-designed tags (DTAG; Mark Johnson) that collected continuous 24 h tri-axial accelerometer and magnetometer data at 1000 Hz from January 1 until mid-February 2017 [71]. Accelerometry data were down-sampled to 25 Hz for further analysis.

5.2 Prediction of behavioral sequences

For all species, available data were divided into discrete non-overlapping time-windows. These intervals were 1 s long for the meerkats and coatis, and 3 s long for the hyenas. Each time-window was labeled with a behavioral category (corresponding to behavioral states), thus predicting behavioral sequences.

With coati accelerometer data, we computed the Vectorial Dynamic Body Acceleration (VeDBA) [72]. VeDBA captures the activity level of an individual. Since VeDBA is bimodally distributed for coatis, we could interpret the two peaks as low- and high-activity states. For each coati, we used a Gaussian Mixture Model with two components to define its activity threshold, and used this threshold to predict its behavioral sequence with the categories low-activity and high-activity.

We predicted more detailed behaviors for meerkats and hyenas using a machine-learning approach. Using previously recorded video data, we generated ground-truth based on a minimal set of behavioral labels corresponding to basic movement states. We then trained random forest classifiers to assign one such movement-state based label to each time-window based on simple kinematic features. Meerkat behavioral labels were foraging, vigilance/resting, and running. Hyena behavioral labels were lying (head down), lying (head up), standing, walking, and running. Additional information about training these classifiers is found in [71] and (see SI Appendix, Text 'Primary data collection and behavioral classifier design')

5.3 Quantifying hazard rates

For each individual, we extracted bouts of each behavioral state from predicted behavioral sequences. To avoid extremely small bouts generated by classifier noise, we considered only sequences that were 2 time-windows or longer. For each possible bout length t, we counted (a) how many bouts were at least t long, and (b) how many bouts were exactly t long. Using these, for each t, we found the proportion of bouts that had gone on for exactly t that stopped within the next time-window. This let us quantify the hazard function, $h(t)$.

One problem with visualizing hazard functions quantified this way is that the resolution of the hazard function worsens as we move right along the x-axis. For this reason, we have visualized only up to the length of the 100th longest bouts from each behavior although all bouts were used to compute the hazard functions. Our visualizations of hazard functions therefore don't span the entire range of bout durations accessible to us. However, this step ensures that we have finer resolution throughout our plots of the hazard function than 0.01.

The 'Running' behavior of the meerkats occurred too infrequently, and in too short bouts, to successfully visualize their hazard functions.

5.4 Fitting and comparing distributions

As above, we extracted bouts of each state for each individual and excluded the 1 time-window bouts. We then fit these bouts to discrete exponential, log-normal, stretched exponential, power-law, and truncated power-law distributions. For fitting, we followed recent statistical developments [17], and used the library powerlaw [73] (v1.5). For each dis-

tribution A, we calculated the log-likelihood

$$\mathcal{L}_A = \sum_{i=1}^{N} \log f_A(X_i),$$

where X_i are the observed bout durations, f_A is the estimated maximum likelihood probability density function for distribution A, and N is the total number of data-points. Using $\mathcal{L}_A$, we then computed the Akaike Information Criterion [74] as

$$\mathrm{AIC}_A = 2\left(\theta_A - \mathcal{L}_A\right),$$

where θ_A is the number of parameters in the distribution A. The distribution with the lowest AIC was chosen as the best-fit distribution.

We only fit distributions if at least 100 bouts of a behavior could be found for an individual. This condition was satisfied by all behaviors in all individuals across all species except the 'Running' state in meerkats, where we could not quantify bout duration distributions with the available number of bouts.

5.5 Quantifying predictivity decay

We quantified how predictive the present behavioral state was of future behavioral states by computing the adjusted mutual information [36] between the time series of behavior and itself lagged by time τ. Adjusted mutual information was found using the python package scikit-learn 1.3.1 [75]. This was done with 30 values of τ spaced equally apart on the log-axis between 1 and 5000. We then fit functions to these data and computed R^2 values for goodness-of-fit comparisons. The functions we fit were an exponential decay ($me^{-\lambda\tau}$), a power-law decay ($m\tau^{-\alpha}$), and a power-law decay with exponential truncation ($m\tau^{-\alpha}e^{-\lambda\tau}$). This was done separately for each individual.

5.6 Ethics

The data used in this study were collected in accordance with institutional ethical guidelines and with approval from relevant local authorities. The collection of data on meerkats was approved by ethical committees at the University of Pretoria, South Africa (permit: EC031-17) and the Northern Cape Department of Environment and Nature Conservation (permit: FAUNA 1020/2016). Research on coatis was approved by the Smithsonian Tropical Research Institute (STRI) Animal Care and Use Committee (IACUC Assurance number 2017-0815-2020). Hyena field methods were approved by Kenya Wildlife Service under permit KWS/BRM/5001 to KEH, and were also approved by the IACUC at Michigan State University under approval PROTO201900126.

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Author contributions

The study was conceptualized by PM and supervised by ASP. VD, LJU, and ASP collected the data on meerkats; EMG, MCC, and BTH collected the data on coatis; and KEH, ASG, and ASP collected the data

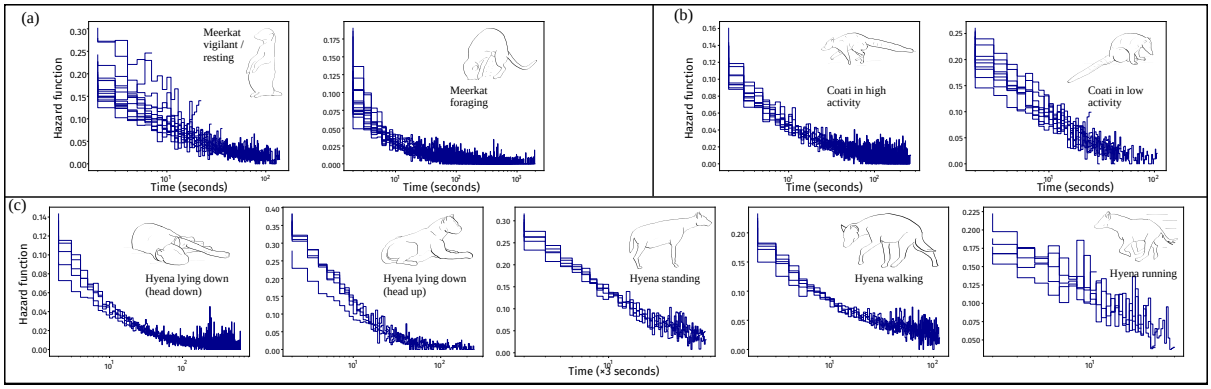

Figure 1: Decreasing hazard functions characterize the bouts of all behavioral states in (a) meerkats, (b) coatis, and (c) hyenas. Each blue line indicates the hazard function of bouts of a single individual. All hazard functions are visualized only up to the length of the 100th-longest bout. For each plot, inset drawings and label indicate the behavior in question. Hazard functions are decreasing across all species, all individuals, and all behaviors. Bouts of the meerkats' running behavior are rare and short leading to an inconclusive visualization of the hazard rate, due to which this state is not included in this figure. x-axes indicate time (in number of time-windows) spent in a bout of a given behavior. Behavioral sequences are inferred at resolutions of 1 s for meerkats and coatis, and 3 s for hyenas.

on hyenas. The meerkat data were collected in cooperation with the Kalahari Meerkat Project, headed by Marta B. Manser, and the hyena data were collected in cooperation with the Mara Hyena Project, headed by KEH. AN, EMG and ASG contributed to labeling of ground truth video data in meerkats, coatis, and hyenas respectively. PM designed systems to infer behavior from accelerometer data, and designed and performed all analyses presented. PM wrote the first draft of the paper with inputs from EMG, VD, and EDS. All authors contributed to and approved the final draft.

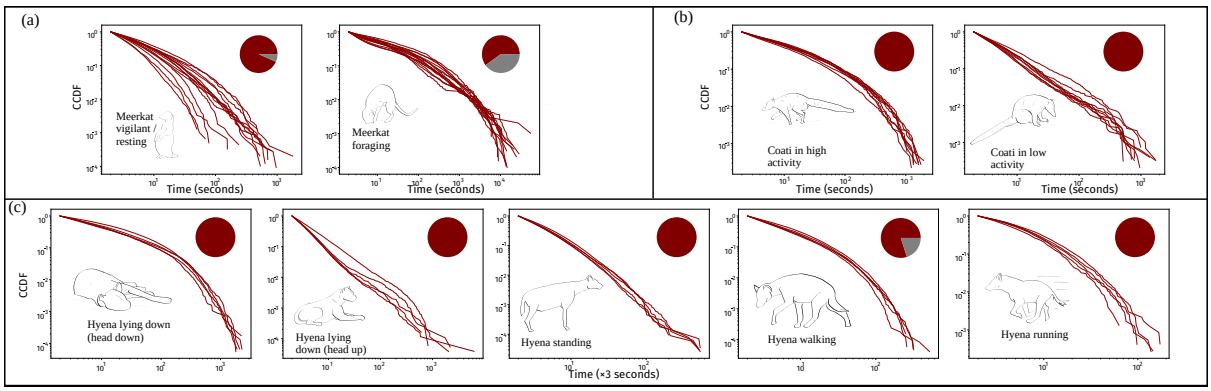

Figure 2: Distributions of bout durations are always heavy-tailed. Panels show observed complementary cumulative distribution functions for (a) meerkats, (b) coatis, and (c) hyenas. All distributions have a heavy tail, as indicated by the nearly linear (on the log scale) relationship between bout duration and frequency for a significant portion of the distribution. For each behavior, all individuals seem to exhibit very similar bout duration distributions. Each sub-plot represents one behavioral state, and red lines represents bout duration distributions from these states for one individual each. Inset line diagrams show the behavioral state, while inset pie-charts show the portion of individuals (in red) that have power-law or truncated power-law bout duration distributions. No behavior showed an exponential fit for any individual (Table S2 lists best fit distributions). x-axes represent duration measured in time-windows (see Methods), and the durations of the time-windows are 1 s for (a) and (b), and 3 s for (c).

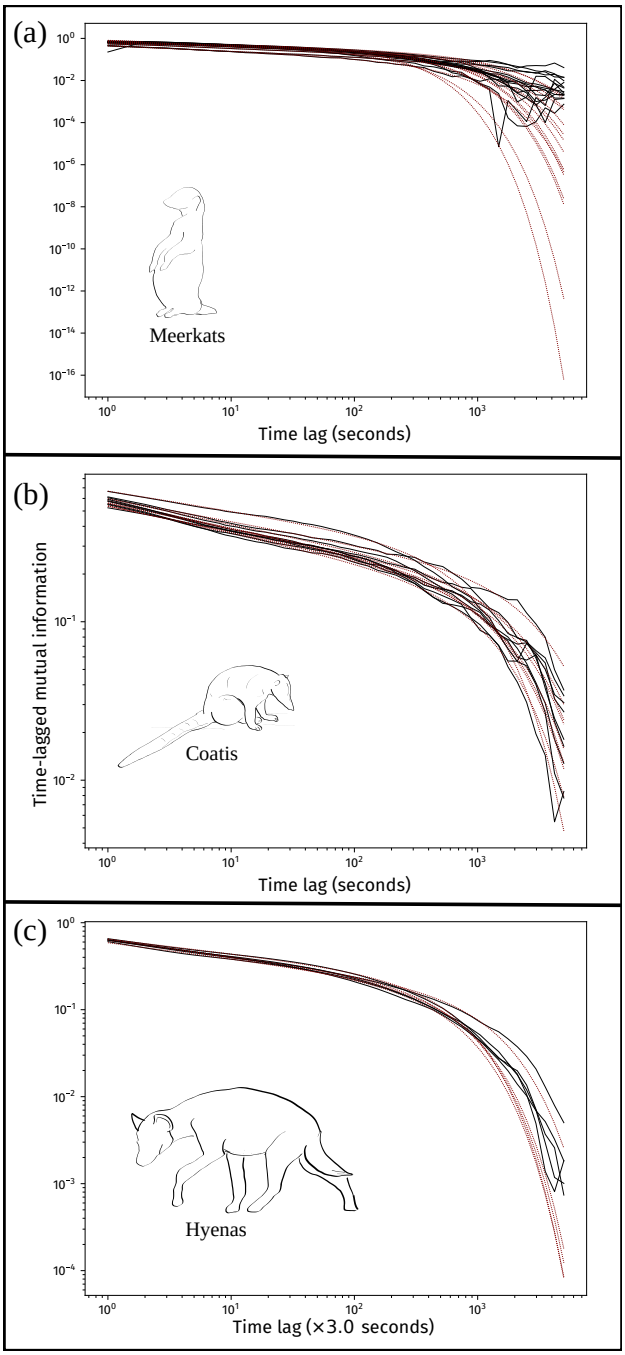

Figure 3: Adjusted mutual information (y-axes) between behavioral states of animals at times t and $t+\tau$, (τ on x-axes) for (a) meerkats,(b) coatis, and (c) hyenas. Adjusted mutual information (black lines for each individual) always fit to exponentially truncated power-laws (maroon lines). Mutual information tends to increase slightly at high lags for meerkats, leading to worse function fits than in the other two species. This increase might be due to some periodicity in meerkat behavior at these high lags, although the exact origin of this increase is still unknown.

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