



25 has intrigued observers throughout the centuries, from Aesop's fables to Romanes's  
26 anthropomorphic anecdotes. However, careful scientific exploration of the mental faculties of  
27 other animals, and their relation to our own, did not commence in earnest until the last century,  
28 with the rise of comparative psychology and ethology. Contemporary comparative cognition,  
29 which grew from these two disciplines, aims to determine the mental processes underpinning  
30 animal behaviour, and to understand how these processes have evolved over the generations and  
31 develop over an animal's lifetime.

32

33 Recent years have seen a great burgeoning of studies of comparative cognition, building on  
34 earlier advances in our understanding of basic processes of perception, attention, associative  
35 learning and memory [4,7]. Elegant experimental work is generating insights into disparate  
36 cognitive abilities across a wide range of taxa, from path integration in ants and spatial memory  
37 in rats [8,9] to mental faculties that were considered uniquely human, such as mental state  
38 attribution and mental time travel in apes and corvids [10–13]. Nevertheless, despite these  
39 important empirical advances, the field suffers from a lack of theoretical underpinning, and  
40 conceptual debates abound. For example, how might we discriminate between alternative  
41 cognitive mechanisms underpinning behaviour? Do the abilities seen in cognitive experiments  
42 reflect domain-specific 'adaptive specialisations' or domain-general problem solving capacities?  
43 How and why do humans differ cognitively from other animals? This special issue brings  
44 together a variety of developmental, mechanistic and functional approaches to the study of  
45 cognition with the goal of synthesizing this emerging body of work, and beginning to build a  
46 theoretical framework to facilitate further progress towards our understanding of animal minds.

47

48 **1. DELVING INTO ANIMAL MINDS: DETERMINING MECHANISMS OF ANIMAL**  
49 **COGNITION**

50 The range of possible mental processes through which animals may interact with their  
51 environments poses a major challenge to students of animal minds. We can observe a non-verbal  
52 creature solving a problem, but how can we infer the processes by which it does so? This issue is  
53 particularly problematic given that seemingly complex behaviour may often be generated  
54 through relatively simple mechanisms. Meerkats, for instance, teach their young to hunt by  
55 responding to age-related changes in pups' begging calls, provisioning dead or disabled prey to  
56 young pups and live prey to older pups. A simple stimulus-response mechanism thus allows  
57 adults to provide pups with prey-handling opportunities appropriate for the pups' age and  
58 competence, without needing Theory of Mind to attribute ignorance to their pupils [14].  
59 Similarly, reflexive responses coupled with associative learning processes enable many animals,  
60 from insects to primates, to use tools effectively without understanding their physical properties.  
61 For example, larval antlions (*Myrmeleon* spp.), insects of the order Neuroptera, knock passing  
62 prey into their pit-traps by flinging grains of sand in response to vibrational cues [15]. How  
63 might we discriminate between such low-level mechanisms and other, more complex cognitive  
64 processes? It may be tempting to assume that species that are more closely related to us may  
65 share more "human-like" cognitive faculties. However, numerous examples of evolutionary  
66 convergence in unrelated taxa, along with abundant evidence of the importance of relatively  
67 simple, evolutionarily ancient mental processes in human behaviour [16–18] caution against this  
68 archaic view of a mental *scala naturae*. Instead, the contributors to this volume urge a more  
69 careful, bottom-up approach to determine the minimal computational requirements needed to

70 generate particular behavioural outcomes and to use careful experimentation to tease apart  
71 alternative explanations.

72

### 73 ***1.1 Bottom-up approaches: building models and robots***

74 It is common in comparative cognition to use folk psychological intuitions of how humans solve  
75 certain problems when designing experiments to test the cognitive abilities of other animals.

76 While this approach has clear value in helping to derive hypotheses, it suffers from two major  
77 weaknesses. First, our intuitions of how we solve problems have repeatedly been shown not to

78 reflect psychological reality (e.g. [19,20]). Secondly, a reliance on folk psychological intuitions  
79 may detract from considering other, arguably more “killjoy” explanations based on simpler

80 mechanisms [17,18]. A fundamentally different approach advocated by some of the contributors  
81 to this issue is to build models of simple neural networks to determine the minimal necessary

82 requirements to solve a specific task. These models often yield rather surprising results,  
83 suggesting that abilities that are commonly considered to be complex may in fact be

84 implemented by very simple networks (see [21], this issue). A circuit of only a few hundred  
85 neurons, for example, has been shown to suffice for reliable face recognition [22]. This approach

86 is clearly of great value in quantifying basic computational complexity, undermining the  
87 assumption that many cognitive feats require big brains [21,23]. Indeed, recent studies have

88 revealed a number of striking cognitive feats in small-brained animals such as insects and, as  
89 Webb discusses in this issue [3], there is evidence that insects may employ internal mental

90 representations of the outside world. However, given that even miniscule invertebrate brains  
91 contain more neurons than the theoretical neural thresholds predicted by computational models

92 for many tasks, this ‘minimal cognition’ approach may be limited in explaining observed

93 cognitive differences between species. Moreover, the computational requirements for solving a  
94 specific, isolated problem may underestimate those needed to solve the same task in the real  
95 world, let alone solve multiple different tasks using the same network. One way to build up  
96 complexity towards that faced by an animal in the physical world is to build a robot that must  
97 replicate the animal's behaviour using the hypothesised neural mechanism to solve a given task.  
98 As Webb points out, robotics thus forces us to face real world difficulties such as perceiving and  
99 attending to relevant stimuli in addition to the abstract computational aspects of a problem, thus  
100 generating more realistic demonstrations of minimal sufficiency. For example, a robotic female  
101 cricket may be able to discriminate between male songs and approach only those who sound like  
102 members of a given species without needing to rely on an internal computational mechanism for  
103 evaluating and comparing songs [3]. Unlike a real cricket, however, it cannot deal with the  
104 additional complexities involved in finding food and avoiding predators. The development of  
105 ever more complex robots, capable of computing solutions to multiple problems, may generate  
106 important insights into the computational requirements needed for biological systems to respond  
107 adaptively to the multitude of challenges they face in their natural environments. A related  
108 challenge is to determine how organisms may integrate currently available information with  
109 previously acquired knowledge of how the world works, bringing all the necessary cognitive  
110 resources to bear when faced with a novel problem. How are parallel processing units in the  
111 brain integrated to create a coherent, structured system capable of responding appropriately when  
112 encountering a problem for the first time? How might a New Caledonian crow (*Corvus*  
113 *moneduloides*) or a rook (*Corvus frugilegus*), for example, have the wherewithal to  
114 spontaneously manufacture a hook to pull up a bucket containing food [24,25]? In this issue,  
115 Shanahan takes a bottom-up approach, drawing on recent advances in brain connectivity to

116 propose a cognitive architecture that can generate such seemingly insightful solutions to novel  
117 problems in the physical world [26]. This consists of a number of discrete modules with  
118 extensive internal connectivity (a “modular small-world network”), which are in turn connected  
119 to one another through nodes known as connector hubs to form a “connective core”. Such a  
120 system may enable the unanticipated integration of mental processes to produce a coherent  
121 sequence of actions to achieve a goal. This theoretical approach thus holds the great promise of  
122 allowing us to move beyond current vague conceptions of insight as a sudden, magical “Eureka  
123 moment”, to a tangible computational process that is amenable to research. An important  
124 question arising from this work is how and why, given that the brains of humans, macaques, cats  
125 and pigeons are all known to possess a connective core, these species may nevertheless differ  
126 radically in their ability to plan their actions when solving a task. Answers to this question will  
127 emerge from a more detailed understanding of differences in neural connectivity in the brains of  
128 different species and their resulting computational power, coupled with behavioural tests of what  
129 different animals are capable of.

130

## 131 **1.2 Top-down approaches: inferring cognitive mechanisms from behaviour**

### 132 *(a) Associative learning as a candidate explanation*

133 For behavioural researchers, a principal challenge is to devise experiments capable of  
134 discriminating between alternative mechanistic explanations for observed behaviour. The  
135 bottom-up approach exemplified by neural network models using computer simulations and  
136 robotics cannot yet provide testable predictions for the range of behaviours examined in  
137 contemporary comparative cognition research. Learning theory, in contrast, is grounded in  
138 behavioural research and provides concrete hypotheses that can be readily examined by

139 empiricists. Indeed, associative learning is found throughout the animal kingdom and is known  
140 to play a role in generating even seemingly complex behaviour in both non-human animals and  
141 in our own species. Nevertheless, associative explanations are sometimes overlooked, perhaps as  
142 a result of knee-jerk reactions to the overambitious claims of behaviourism, leading to a focus on  
143 what Heyes [17] calls “super-cognitive” explanations derived from folk psychological intuitions.  
144 In fact, modern learning theory is considerably more nuanced than the caricature of  
145 behaviourism would suggest. Unlike behaviourism, it does not claim that anything can be  
146 learned (or that all behaviour is learned), but instead incorporates constraints that limit learning  
147 of coincidental associations and promote learning of biologically relevant associations.  
148 Moreover, learning theory has the distinct advantage over folk psychology in that it rests on  
149 well-described, general theories such as the Rescorla-Wagner [27] and Mackintosh [28] models.  
150 One interesting development discussed by Dickinson [29] is his ‘associative-cybernetic’ theory  
151 [30,31] which postulates that, if embedded in a constraining processing architecture, associative  
152 learning may give rise to rational goal-directed action. That is, rather than simply learning that a  
153 certain action is rewarded, an animal may also learn that its action causes a specific beneficial  
154 outcome. This theoretical prediction has considerable empirical support. For example, rats  
155 trained to obtain a reward by pressing a lever will reduce their lever pressing if the value of the  
156 reward is reduced, indicating that they represent the causal relation between their own lever-  
157 pressing actions and the outcome (reviewed in [29]). Thus, associative learning theory provides a  
158 powerful and tractable framework for research on animal (including human) minds. Indeed,  
159 rigorous research in comparative cognition often uses associative learning as a null hypothesis,  
160 making considerable efforts to derive candidate explanations from learning theory to be tested  
161 through behavioural experiments (e.g. [32]). There will, of course, be instances when behaviour

162 cannot be understood purely in terms of associative processes. Human behaviour, for instance, is  
163 guided to a large extent by reasoning and inference about abstract causal relations in the physical  
164 and social worlds [33–35]. The possibility that animals may employ similar cognitive processes  
165 has attracted great interest from students of animal minds, but lacks the theoretical grounding of  
166 associative theory and so is more difficult to pin down. If associative processes are found to be  
167 lacking as explanations of animal behaviour, how might we make progress in determining  
168 alternatives?

169

170 *(b) Beyond associative learning: individual-level approaches*

171 One common and powerful experimental approach is to use a series of training trials in which  
172 subjects learn the basic requirements of the task, followed by transfer tests in which the causal  
173 properties of the problem are kept constant, but arbitrary visible stimuli are changed. Thus, in  
174 theory, subjects that have learned a simple rule based on visible features will fail transfers, while  
175 those that have abstracted a generalizable understanding of the causal structure of the task should  
176 apply it to solve the transfer [36, 37]. However, as Thornton & Lukas point out, the fact that  
177 transfer tests typically involve the same binary choice over multiple trials means that a subject  
178 might learn a rule based on the visible properties of the transfer test itself [38]. Thus, subjects  
179 may reach a given criterion (say nine correct trials out of ten) using nothing but associatively  
180 learned rules. Conversely, reliance on crude binary criteria of success or failure leads us to  
181 ignore potentially valuable data. Instead, several of the contributors to this issue advocate a more  
182 fine-grained analytical approach that focuses specifically on individual differences in  
183 performance on a trial by trial basis to shed light on the cognitive mechanisms employed when  
184 solving tasks [33,38,39]. Seed and colleagues, drawing on insights from developmental

185 psychology, point out that a detailed focus on individual behaviour, taking into account failed  
186 trials as well as successes, may provide valuable insights into why subjects may fail, and the  
187 precise mechanisms required for success. Using this approach, they show that chimpanzees (*Pan*  
188 *troglydtes*) that failed a task requiring them to discriminate between a complete and a broken  
189 tool failed not because of an inability to represent “connectedness” but rather because of  
190 limitations in memory and attention [33]. Thus, an individual-based analytical approach may  
191 allow us to determine the set of cognitive processes that must be employed together when  
192 solving tasks.

193

194 The individual-level approach may also benefit from using formal planning theory used in  
195 artificial intelligence (AI) research. In this issue, Chappell & Hawes explored a four-trap variant  
196 of the classic ‘trap tube’ test in which the precise characteristics of the task (e.g. which of the  
197 four traps was functional) varied systematically across a series of 64 trials. Using an AI planning  
198 language, they generated a series of possible computational rules or “plans” an animal could  
199 employ to solve the task. They then simulated how each of these plans would perform in each of  
200 the different trials, and compared these simulations to the actual trial-by-trial performance of  
201 orangutans (*Pongo pygmaeus*) [39]. The advantage of this method is two-fold. First,  
202 decomposing the problem into its constituent parts may be valuable in designing experiments.  
203 Second, in common with Seed et al.’s approach, it forces us to move away from the simplistic  
204 and statistically problematic [38] dichotomy of success and failure and instead to harness the rich  
205 data emerging from all the actions of all individuals in all trials to assess how animals solve  
206 problems. In the future, we hope that such individual-based approaches will be combined with  
207 insights from learning theory to determine the role of associative processes in within-task

208 learning, and to discriminate between alternative mechanistic explanations. We also envisage  
209 great potential in linking this top-down approach of decomposing and simplifying specified  
210 problems with bottom-up approaches that specify the components and connectivity of the  
211 computational systems implementing the solutions. For instance, specifying the computational  
212 components and connectivity of a neural system (c.f. [26]) may allow us to constrain the possible  
213 range of plans the system might implement to solve a cognitively challenging task in a  
214 biologically realistic way.

215

## 216 **2. THE EVOLUTION OF ANIMAL MINDS**

### 217 *2.1 Fitness consequences of individual cognitive variation*

218 Through a combination of experimental and theoretical approaches, comparative cognition is  
219 beginning to provide important insights into the mental processes of different animals. However,  
220 existing approaches tend to place relatively little emphasis on the central goal of understanding  
221 how these processes evolve. In this issue, Thornton & Lukas point out that researchers  
222 commonly assume that the cognitive traits they find in laboratory animals are the adaptive  
223 products of natural selection, but they very seldom assess whether the basic tenets of Darwinian  
224 theory apply to the trait in question [38]. For natural selection to act, there must be heritable  
225 variation in the trait, leading to variation in reproductive success [40]. Consequently, if we want  
226 to understand how cognitive traits evolve, we must ask whether they vary between individuals,  
227 are heritable and influence fitness. Laboratory studies commonly reveal substantial variation in  
228 individual performance, but rarely consider its causes. Thornton & Lukas's meta-analyses of  
229 individual performance across a series of cognitive tasks suggest that much of this variation may  
230 be explained by laboratory rearing conditions, with enculturated individuals with extensive

231 previous experience of laboratory tests typically outperforming the rest [38]. It is therefore  
232 unclear to what extent this variation may be heritable, or indeed how cognitive traits may be  
233 manifested in the natural conditions in which they evolved. In some short-lived animals it may  
234 be possible to explore cognitive evolution using selection experiments in the laboratory [41], but  
235 for many of the birds and mammals of interest to students of comparative cognition, such  
236 experiments are less feasible. Laboratory studies must therefore be complemented by field  
237 research to examine links between individual cognitive variation and reproductive fitness.  
238 Unfortunately, the difficulties in examining cognition in the wild have led to a recent trend for  
239 field researchers to assume that individuals that succeed in any experimentally presented  
240 “problem-solving task” possess elevated cognitive abilities, without testing the underlying  
241 mechanisms. Given this trend, there is a danger that, for example, the action of a pigeon pecking  
242 a key to obtain a reward in the field would be regarded as a measure of “cognition”, while no one  
243 would consider the same action to be cognitive if done in a laboratory setting. If field studies are  
244 to provide productive insights into cognitive evolution, it is therefore critical that they  
245 incorporate the valuable lessons of psychological research concerning cognitive mechanisms into  
246 the task design. For instance, Visalberghi and colleagues have used elegant experiments inspired  
247 by laboratory tests of physical cognition to establish that capuchin monkeys recognise the  
248 physical properties that render objects for use as hammers to crack nuts [42]. Similarly, studies  
249 by Healy and colleagues have elegantly adapted laboratory tests of spatial memory and timing  
250 for use in the field (reviewed in [43]), while Cheney & Seyfarth, McComb and others have  
251 devised tests of social cognition incorporating expectation violation paradigms from  
252 developmental psychology [44,45]. Such experimental approaches, as well as novel statistical  
253 tools allowing mechanisms of learning and cognition to be inferred from natural behaviour [46]

254 hold great promise in enabling us to understand the cognitive processes used by animals in their  
255 environments. A key challenge now is to determine whether individual animals in the wild vary  
256 in their cognitive abilities, to use advances in quantitative genetics to assess the heritability of  
257 this variation and to begin to examine its fitness consequences.

258

259 It may be tempting to assume that elevated cognitive abilities ought always to confer fitness  
260 benefits, and are therefore subject to positive selection. However, any benefits associated with  
261 improvements in cognition will be balanced against the costs they may carry. In *Drosophila*, for  
262 example, there is evidence that selection for improved associative learning abilities among adults  
263 comes at a cost of reduced ability to compete for food resources at the larval stage [47]. In  
264 addition, at the individual level, the potential benefits of cognition will depend on behavioural  
265 phenotypes. As Sih & del Giudice discuss in this issue, there is extensive evidence that  
266 individual animals differ consistently in their behaviour over time and across contexts, and this  
267 behavioural consistency may place important constraints on the ways in which cognitive abilities  
268 are manifested [48]. Consider, for example, two individuals that have equal cognitive abilities  
269 but differ in their behaviour, with one being very bold and exploratory while the other is shy and  
270 slow to investigate unknown places or objects. While the bolder individual is likely to encounter  
271 novel stimuli more often, the shier individual may have a greater tendency to pause and attend to  
272 changes in the environment and update its assessment of a given situation. Behavioural  
273 differences may therefore generate a trade-off between speed and accuracy when dealing with  
274 novel problems, and influence the benefits that individuals can derive from their cognitive  
275 abilities.

276

277 Just as individuals commonly exhibit suites of inter-correlated behaviours (termed “behavioural  
278 syndromes” [48]) they may also exhibit consistency in cognitive abilities across different  
279 contexts. Indeed, there is a longstanding debate as to whether animal behaviour is underpinned  
280 by cognitive specialisations that have evolved to fulfil specific ecological functions (e.g.  
281 retrieving cached food [49–51]), or rather is governed by domain-general mechanisms that  
282 operate across contexts. Herrmann and Call, using large datasets of the individual cognitive  
283 performance of chimpanzees across a test battery of multiple different tasks, suggest that the  
284 truth may lie somewhere in between the two views [50]. Their analyses reveal that while some  
285 exceptional chimpanzees consistently outperformed their conspecifics across a range of tasks,  
286 there is no evidence for one single “general intelligence” factor, but neither were performances  
287 entirely unrelated across different tasks. Rather, the data appear to support the existence of a  
288 number of distinct clusters of abilities, such as spatial knowledge and discrimination learning  
289 [52]. Further work is needed to determine whether the cognitive abilities of other organisms will  
290 exhibit similar clustering, but the evidence from chimpanzees suggests that there may be  
291 common mechanisms that animals apply to different tasks within particular clusters of abilities.  
292 An understanding of cognitive evolution will therefore benefit from explicit theoretical models to  
293 consider not only how overt, measurable behavioural abilities evolve, but also how selection may  
294 act on the underlying mechanisms [53].

295

## 296 *2.2 Modelling the evolution of cognitive mechanisms*

297 As Lotem & Halpern discuss, rigorous theoretical analyses of cognitive evolution must consider  
298 how different components of cognitive processing interact and co-evolve [54]. For example, to  
299 understand how learning mechanisms evolve, we must also consider the evolution of the

300 attentional and motivational mechanisms. Whereas traditional learning models assume that data  
301 are presented to the animal as discrete, distinguishable stimuli, Lotem & Halpern's model  
302 explicitly considers the fact that animals must sift through and obtain relevant information from  
303 the morass of data in their environments. The model assumes that, when animals encounter  
304 biologically relevant stimuli such as food, they will also attend to other information in the  
305 immediate environment. This array of data is then compared to previously encountered datasets.  
306 Segments of data that are rarely encountered tend to be forgotten and decay, while links between  
307 commonly encountered segments increase in weight and may become fixed in memory. Thus, by  
308 segmenting and linking chunks of data according to encounter rates and allowing irrelevant data  
309 to decay, the animal may build up a structured representation of the environment without the  
310 heavy computational burden of learning and remembering connections between all possible  
311 segments of data. Natural selection may act to tweak the parameters of both the data acquisition  
312 and learning mechanisms, resulting in organisms that are well adapted to handle the natural  
313 distribution of biologically relevant data in their environment. Lotem & Halpern argue that this  
314 process of co-evolution of data acquisition and learning may generate incremental cognitive  
315 change, allowing organisms to extract relevant data even when faced with dynamic and complex  
316 arrays of information such as those that characterise some social systems. In their view, this  
317 process might even facilitate key human cognitive characteristics such as theory of mind and  
318 language acquisition [54–56].

319

### 320 **3. THE QUESTION OF HUMAN UNIQUENESS**

321 Of course, the quest to understand how and why the cognitive abilities of our own species may  
322 differ from those of other animals has long been a central motivating force for much of  
323 comparative cognition. What cognitive processes make us unique, and what are the origins of  
324 these processes? As Shettleworth discusses in her contribution to this issue, there have been a  
325 multitude of theories of human uniqueness throughout the years [57]. Some of these suggest that  
326 the difference between humans and other animals lies in broad, domain-general processes that  
327 are manifested across a wide range of behavioural contexts [58,59]. In contrast, evolutionary  
328 psychologists have tended to view human cognition as comprising a suite of discrete modules,  
329 some of which may exist in our species alone [60]. Both of these approaches appear to  
330 emphasise dichotomous distinctions between “us and them”. Is a given cognitive faculty (be it  
331 domain-general or specific) uniquely human, or might it be found in other animals? Such human  
332 vs. non-human comparisons suffer from two main problems. First, comparative studies have  
333 tended to apply tests designed for adult, verbal humans and thus may often risk underestimating  
334 the abilities of non-verbal creatures [61]. Second, an emphasis on the presence or absence of  
335 particular cognitive capacities may detract attention from the possibility that, even if an animal  
336 fails a test of some human ability, some of the cognitive processes it applies may still be shared  
337 with humans. Instead, Shettleworth [57] and Spelke [35] argue that important insights may lie in  
338 examining the development of cognitive abilities over individual lifetimes. Just as in  
339 evolutionary biology it is recognised that seemingly different traits may share important  
340 developmental commonalities [62], it is increasingly clear that considering developmental  
341 cognitive trajectories may reveal important elements of similarity and difference. For example,  
342 experiments by Spelke and colleagues [35] suggest that human spatial cognition develops in two  
343 distinct stages. From infancy, children exhibit two systems for representing objects and vectors.

344 These are largely shared with other animals and are thus likely to be evolutionarily ancient  
345 cognitive adaptations for navigation. Later in development, the acquisition of language and  
346 culture enables children to combine the two systems in uniquely human ways to form abstract  
347 geometrical concepts (reviewed in [35]). Tomasello, Call and colleagues place a similar  
348 emphasis on developmental processes as being at the heart of human socio-cognitive uniqueness  
349 (reviewed in [63]). Their extensive comparative experiments suggest that while human children  
350 and apes show similar performance on tests of physical, spatial and numerical cognition, children  
351 typically outperform apes on social tasks. In particular, they argue that, unlike our closest  
352 relatives, humans are endowed from an early age with the motivation to engage with others in  
353 joint activities involving shared goals and attention. Later in development, this tendency  
354 facilitates the use of linguistic symbols and the creation of cultural norms [52,64,65]. As these  
355 examples show, a continued emphasis on developmental processes in comparative cognition is  
356 likely to yield further important insights into the similarities and differences between humans  
357 and other species. To fully take advantage of this approach, it is important to extend the current  
358 focus on comparing children with adult non-human animals to compare developmental  
359 trajectories across species, acknowledging the fact that non-human cognition also develops.  
360 Indeed, a common theme of this issue is that, as the field of comparative cognition matures, it  
361 must incorporate careful comparative analyses across all levels - within individual lifetimes,  
362 between individuals and between species. Understanding animal cognition is a deeply  
363 challenging endeavour, not least because it requires investigation of multiple layers, from genes  
364 and neurones to computational processes and the resulting behaviours to the developmental and  
365 evolutionary processes shaping cognition over time. We hope that a synthesis of empirical and  
366 theoretical tools from fields including robotics, neuroscience, psychology and biology, such as

367 those showcased in this issue, will help future research further unravel the mysteries of animal  
368 minds.

369

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378

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