1 **Individual and ecological heterogeneity promote complex communication in social vertebrate group**

2 **decisions**

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4 Authors:

5 Christophe Bousquet[1,2], Cédric Sueur[3,4], Andrew King[5], Lisa O'Bryan[6]

6 1 Department of Psychology, University of Konstanz, 78457 Konstanz, Germany

7 2 Cluster for the Advanced Study of Collective Behaviour, University of Konstanz, 78457 Konstanz,

8 Germany

9 3 Université de Strasbourg, CNRS, IPHC UMR 7178, F-67000 Strasbourg, France

10 4 Institut Universitaire de France, Saint-Michel 103, F-75005 Paris, France

11 5 Biosciences, Faculty of Science and Engineering, Swansea University, Singleton Park, Swansea SA2

12 8PP, UK

13 6 Department of Psychological Sciences, Rice University, Houston, Texas

14

15 ORCID IDs:

16 CB: 0000-0003-1650-8004; CS: 0000-0001-8206-2739;

17 AK: 0000-0002-6870-9767; LO: 0000-0002-8878-7674

18

19 **Abstract**

20 To receive the benefits of social living, social animals must make effective group decisions that enable

21 them to achieve behavioural coordination and maintain cohesion. However, heterogeneity in the

22 physical and social environments surrounding group decision-making contexts can increase the level

23 of difficulty social organisms face in making decisions. Groups that live in variable physical

24 environments (high ecological heterogeneity) can experience barriers to information transfer and

25 increased levels of ecological uncertainty. In addition, in groups with large phenotypic variation (high

26 individual heterogeneity), individuals can have substantial conflicts of interest regarding the timing

27 and nature of activities, making it difficult for them to coordinate their behaviours or reach a

28 consensus. In such cases, active communication can increase individuals' abilities to achieve

29 coordination, such as by facilitating the transfer and aggregation of information about the

30 environment or individual behavioural preferences. Here, we review the role of communication in

31 vertebrate group decision-making and its relationship to heterogeneity in the ecological and social

32 environment surrounding group decision-making contexts. We propose that complex communication

33 has evolved to facilitate decision-making under specific socio-ecological contexts, and we provide a

34 framework for studying this topic and testing related hypotheses as part of future research in this area.

35

Introduction

Group living provides animals with benefits and challenges [1]. Benefits include a reduced likelihood of being preyed upon [2], increased access to mates and cooperative care of offspring [3], as well as improved access to food and other resources [4]. However, in order to reap these benefits, group members have to maintain cohesion [1], which can be challenging because of heterogeneity in both an individual's physical and social environments [5].

Physical environments with high levels of heterogeneity can constrain information transfer and increase ecological uncertainty. According to the 'habitat constraints hypothesis' [6,7], effective group decision-making should be more difficult to achieve in environments with high ecological heterogeneity [8] (**Fig. 1a**). Indeed, whilst simple copying of motion among group members can enable groups to navigate and make decisions in environments that are homogeneous and predictable, this becomes more difficult in heterogeneous environments where visual information can be reduced [9] and acoustic information can be attenuated or distorted [10,11] (**Fig. 1a**). Even though not the focus of our paper, these physical constraints may also select for redundant signals, in which complexity may reduce errors in signal transmission to ensure good signal perception by receivers, rather than to increase the amount of information content per se [12]. Additionally, where important resources are highly heterogeneous (e.g., variable food patch sizes: [13]), group members can have difficulty finding a location that provides access to resources suitable for all [6]. Thus, not only is information transfer constrained, but fission and fusion (joining and splitting of the group) may become necessary for individuals to access key resources (9), further increasing the complexity of decision-making.

Cohesion can also be difficult to achieve when there is high individual heterogeneity within groups. According to the 'individual heterogeneity hypothesis' [14,15], animals will struggle to achieve synchrony when they are of different sizes, ages, sexes, reproductive states, or dominance levels, as these differences will result in differences in their physiology, cognition and behaviour [15], nutritional requirements [16] and optimal activity patterns [6,17] (**Fig. 1b**). For example, when individuals in a group differ in locomotor capacity, some group members will either have to move faster, slower, or make more frequent pauses to keep the group together, or risk group fission [18] as shown in species ranging from fish to baboons [6,19]. Activity differences between sexes can also drive social segregation in many ungulate species [8,17,20] since males have to move more frequently to meet their nutritional needs [21]. Maintaining cohesion when there are large conflicts of interest among individuals can therefore be difficult, and this is seen in a wide variety of species [15], ranging from ants [22] and fish [23] to primates [24]. Finally, group size in itself can be a component of individual heterogeneity, as additional group members are unlikely to have similar needs or characteristics. For example, group size has been shown to be a more significant driver of the diversity of vocal, olfactory, and visual signals in lemurs compared to environmental factors such as habitat type or the number of

71 conspecific species [25]. Therefore, achieving group coordination and making collective decisions is

72 challenging when groups live in environments that are highly heterogeneous and/or when their group

73 composition is highly heterogeneous.

74 A variety of communication systems have evolved that can aid group cohesion and coordination within

75 given social and ecological environments. The two most common modes of communication used to

76 coordinate collective decision-making in vertebrates are acoustic [26,27] and visual [28,29]. These

77 modes of communication are particularly suited to the context of movement [26] or social foraging

78 [30] since vocal and visual signals are easily locatable and can be changed rapidly (in contrast to

79 olfactory communication). In this perspective article, we discuss whether and how visual and vocal

80 signals may facilitate cohesion and efficient collective decisions under specific socio-ecological

81 contexts. In particular, we explore the idea that the complexity of the communication used in a given

82 collective decision-making context is positively related to the level of ecological and individual

83 heterogeneity surrounding this decision: **Fig. 1**. Complexity can be assessed along 3 axes (diversity,

84 flexibility and combinability) [31], which are also relevant for understanding heterogeneity. Thus, in

85 section **Studying the role of ecological and individual heterogeneity in communication and collective**

86 **decision-making**, we propose measuring both communication complexity and individual and

87 ecological heterogeneity using this unifying framework. Note that when we discuss complexity and

88 heterogeneity, we mean the amount of variability present that is behaviourally or physiologically

89 relevant for receivers [12,32–35]. For example, the same ecological environment may be perceived

90 differently by different species, thereby impacting its apparent heterogeneity [36–38]. To achieve this

91 comparison, ecological heterogeneity needs to be measured at a high-resolution and then determine

92 which resolution level is most pertinent for which species (i.e., when perceived heterogeneity becomes

93 informative for the species under study) [38,39]. The same argument can be applied to individual

94 heterogeneity and communication complexity. For instance, high resolution measures of

95 communication complexity may indicate that group signatures exist in a given species, but such

96 complexity may not be attended to by individuals of this species [40].

97 In contrast to many studies which have examined relationships between species- or habitat-wide

98 heterogeneity and repertoire-wide communication complexity [25,41,42], we focus on the

99 relationships between socioecological heterogeneity and communication complexity at the level of

100 given group decision-making events. This focus is important because each event has its own social and

101 ecological characteristics that are relevant for understanding the specific decision-making challenges

102 the group may face. Therefore, required measures of ecological and individual heterogeneity may

103 differ between collective decision contexts (e.g., transitioning between activities, foraging

104 coordination, coordinating group movement…). Since group decision-making contexts may involve

105 many group members, a variety of decision types, variable environments, and ever-changing

106   individual-level motivations, they have the potential to be more dynamic than other well-studied

107   communication contexts, such as mate-choice or predator detection [32,33,35]. By leveraging new

108   technologies that can track these dynamic changes, we can gain a more fine-grained understanding of

109   the relationship between socioecological variables and communication complexity during given

110   decision-making events. This focus not only enables a better understanding of species differences in

111   evolved communication mechanisms, but also the flexibility of communication used by a given species

112   or social group.

113   In the sections that follow, we first discuss the types of information transfer and decision-making

114   mechanisms animal groups use under different socio-ecological contexts (varying in levels of individual

115   and/or ecological heterogeneity: **Fig. 1**). Throughout we focus on social vertebrates with an emphasis

116   on terrestrial mammals, but the principles we discuss have been studied, and are relevant, across taxa.

117   Second, we provide a more formal description of the links between both ecological and individual

118   heterogeneity and communication complexity during group decisions. Finally, we discuss how new

119   technologies can enable researchers to explicitly study behaviour and information transfer in real-time

120   – which is necessary when studying dynamic communication processes.

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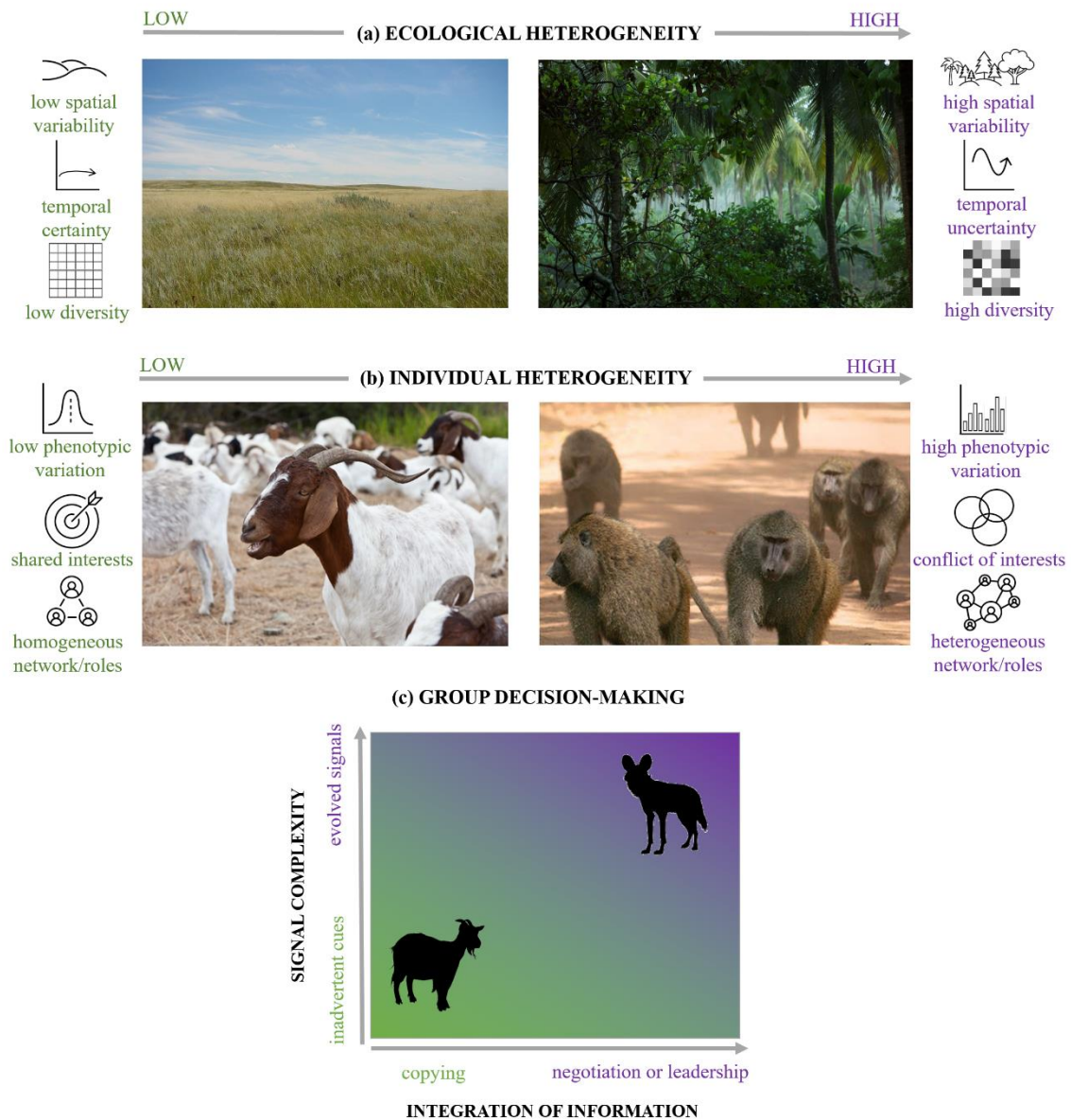
Figure 1. (a) Ecological heterogeneity, defined broadly as the spatial variation in land cover and vegetation (habitat) [9,43], the temporal variation of resources and climate (environment) [44–46], and species diversity [47,48]. For example, whilst grasslands (pictured, licensed under CC BY-SA) have complex height structures (within individual patches of grassland) and there is variability between the patches (i.e., different species), we consider grassland to have low ecological heterogeneity from the perspective of a grazing ungulate herd. In contrast, a tropical rainforest (pictured, licensed under CC BY-SA) has high spatial variability in vegetation (canopy height, land cover) and greater temporal uncertainty in resources, and these non-uniformities create opportunities for higher biodiversity. **(b) Individual heterogeneity**, defined as differences in phenotype, interest, or social interactions/roles. For example, primate troops (baboons pictured, licensed under CC BY) have high phenotypic variation

133   (e.g., different ages, sexes, female reproductive states) [15] and these differences result in conflicts of

134   interest [16,49], heterogeneous interaction networks, and specific social roles (e.g., dominance ranks,

135   leader-follower dynamics) [50,51] resulting in high individual heterogeneity. Ungulate herds (goats

136   pictured, licensed under CC BY) represent social systems with lower individual heterogeneity because

137   whilst sexual dimorphism can result in conflicts of interest [20,52], phenotypic variation tends to be

138   lower [53], and so individuals have more shared interests, more homogenous interaction networks,

139   and weaker social hierarchies. **(c) Group decision-making** requires that individuals use social

140   information and reach consensus on the timing and nature of their activities [24,54,55]. In cases when

141   individual heterogeneity and ecological heterogeneity are positively correlated (green = both low,

142   purple = both high) [56], we expect that this synergy should select for different decision-making

143   mechanisms with regards to how groups convey (y axis) and integrate (x axis) information when

144   reaching consensus. We propose that simple copying of inadvertent cues (e.g., neighbour motion) can

145   underlie group decisions in contexts associated with low heterogeneity (e.g., goat travel directions)

146   [57], whilst complex signals and integration mechanisms (e.g., vocalizations and quorums) can underlie

147   the negotiation of group outcomes in high heterogeneity contexts (e.g., African wild dog decisions to

148   begin hunting) [58]. In cases when individual heterogeneity and ecological heterogeneity are not

149   positively correlated (e.g., when individual heterogeneity is high but ecological heterogeneity is low),

150   we expect to find group decision-making mechanisms of intermediate complexity.

151

Decision-making contexts and the role of communication

We propose that the complexity of information transfer and communication in group decision-making contexts can be studied by considering two linked processes. First, the information transfer itself can be more or less complex (**Fig. 1c** vertical axis). Information transfer among group members by inadvertent cues [59,60] (e.g., through social facilitation or enhancement) can be considered simpler than signals that evolved due to the change in behaviour they elicit in receivers. The context of predator detection is useful for understanding the difference between a cue and signal. If a group member detects a predator, it may produce a startle response or flee (i.e., a cue), which inadvertently provides information to neighbours that a dangerous stimulus has been detected [61–63]. Alternatively, an individual may produce an alarm call (i.e., a signal) upon detection of a predator, which is a signal that evolved in some species specifically for the purpose of informing group members about the presence, and perhaps traits, of the predator [64–66]. In addition to the differences between signals and cues, signals themselves can range in complexity, from simple movement pauses to elaborate visual displays or from simple calls to semantic acoustic sequences [67]. Second, the decision-making mechanisms used by group members to integrate the information derived from cues or signals can be more or less complex (**Fig. 1c** horizontal axis). For example, copying behaviour (or mimetism) [68] can be considered less complex than a process whereby individuals signal their preferred actions and groups reach consensus by a quorum decisions (or voting) [26,58,69,70], which is thought to require a different type of cognitive ability [71]. Thus, the cognitive complexity of a species may restrict how communication signals can be integrated, highlighting the importance of considering phylogenetic constraints when making comparisons across species. Although out of the scope of our perspective, dedicated reviews have highlighted the importance of these and other constraints [56,72–74].

Below we describe different behavioural and communication mechanisms used to coordinate group-wide behaviours in three key contexts: transitioning between activities, foraging coordination, and coordinating group movements. These are among the most studied collective decision-making contexts that are absent of interference from other competing groups or predators and are therefore likely to better capture the effects of individual and ecological heterogeneity on how groups make decisions. Within each of these contexts, we outline how information may be shared inadvertently in the form of cues [57,75,76] or actively transferred by signals of varying complexity that were selected for this purpose [26,28,58]. In each context we describe, we first explain situations in which coordination and group decisions can be achieved via both simple cues and simple integration mechanisms (e.g., copying), followed by scenarios that are associated with more complex signals and/or signal integration mechanisms.

Transitioning between activities

To maintain the benefits of cohesion, group members must coordinate their transition between activities, especially when transitioning between stationary activities and movement. A variety of behavioural and communication mechanisms can be used to coordinate this transition. The most straightforward may be to follow the movement initiation of a given group member. For instance, collective departures in goats (*Capra aegagrus hircus*) emerge from individuals copying one another's motion (i.e., a cue), and all individuals can initiate movement without hierarchical leadership [57]. A similar mechanism is at play in European bisons (*Bison bonasus*), except that adult females have more weight in collective departures [76]. However, in some species, signals can be added in certain social and ecological contexts to enhance leadership. For example, in rhesus macaques (*Macaca mulatta*) [28], Tonkean macaques (*M. tonkeana*) [28], and white-faced capuchin monkeys (*Cebus capucinus*) [77], simple copying behaviour is often combined with visual signals, such as pauses and backward glances. When starting to move, departing individuals use these signals to "recruit" group members to join their decision to transition from rest to movement. When transitioning between activities not only requires recruitment of others, but also a consensus decision, signals are critical. Specialized vocalizations [26] or vocalizations diverted from their original function [58] may all be used to communicate individual preferences with regard to the timing or direction of departure [52]. Typically, a certain number of individuals (i.e., a quorum) need to communicate their preference for a group to make a consensus decision. Whilst the quorum number can be quite small (three in meerkats, *Suricata suricatta,* [26] or about 30% of the group in macaques [78]), quorum decisions allow groups to maintain their cohesion. In addition, this type of decision-making can permit adaptive tuning of the trade-off between decision speed and accuracy [70], which is also common, for instance, in ant collective decisions [79].

Foraging coordination

Coordinating social foraging requires a mix of coordination mechanisms, including choosing a food patch, keeping track of group members while foraging, and deciding when to collectively transition between food patches. In some contexts, behavioural cues may be enough to coordinate foraging. For example, in some species, foraging sites may be decided by individuals who benefit most from foraging in a given location [51]. Such despotic leadership can be an effective means of coordination, but it can also come with large consensus costs for other foragers if the chosen foraging location is not suitable for all, which can result in the fission of the group [51]. Producer-scrounger foraging dynamics represent another means by which foragers opportunistically coordinate their foraging through behavioural cues. Here, the act of finding food and beginning to forage can provide cues to others that the producer's location represents a productive feeding site, prompting approach by scroungers [80].

222   In addition to simple cues, foraging coordination may be achieved via active signals, such as food-
223   associated vocalizations. One function of these vocalizations is the attraction of group members to the
224   signaller's feeding site [81]. This active recruitment signal can shape group decision-making by sharing
225   information about the quality of food, or simply the signaller's intention to feed in a given location
226   [82–84]. Other food-associated vocalizations are thought to advertise the location of the signaller's
227   specific feeding site while foraging, modulating group cohesion by promoting sufficient spacing among
228   foragers [85]. In addition, some food-associated vocalizations may reflect the signaller's foraging
229   success (or lack thereof) at a given foraging site. This information can be used by social foragers when
230   making consensus decisions regarding the timing of departure from a foraging patch [26,86,87].
231   Indeed, such a mechanism can enable social foragers to better collectively estimate the quality of a
232   foraging patch, reducing the cost of foraging socially [87,88].

233

234   *Coordinating group movement*

235   Group-living animals have to coordinate their positions and trajectories while traveling, or else risk
236   becoming separated. A common method by which many species coordinate active movement is by
237   responding to the movement behaviours of their neighbours (i.e., cues). For example, simply aligning
238   one's trajectory with close neighbours, avoiding getting too close and moving towards far away
239   neighbours can maintain many coordinated group movements [89]. However, subsets of group
240   members may also produce vocalizations to modify the movement trajectory. For example, when a
241   group member is at high risk of becoming separated, loud contact calls (i.e., "lost calls") may be
242   produced by isolated members. When group members hear these signals, they generally either move
243   towards them [90], slow down movement away from them [27], and/or respond vocally so that the
244   separated individual can rejoin the group [91]. In addition, some species, such as white-faced
245   capuchins, produce vocalizations that prompt the group to move in the direction travelled by the
246   signaller as a means of influencing group direction [92]. Group movement may additionally be
247   coordinated by regularly produced low-intensity calls, which are typically termed "contact calls" or
248   "close calls." These vocalizations are often individually identifiable and thought to enable group
249   members to acoustically monitor the positions of their fellow group members in the absence of, or in
250   addition to, visual information. Contact or close calls are common call types, sometimes occurring as
251   often as every 5-20 seconds [40] and varying with activity [93,94], environment [94], and/or the
252   spacing between individuals [95]. Such calls are usually of low intensity in order to generate a
253   soundscape background that can be interrupted by more urgent signals. While these vocalizations do
254   not elicit obvious behavioural reactions, they may facilitate subtle changes in the orientation [93],
255   proximity [96], and/or vocalization behaviour of receivers [97] which, together, are thought to aid in
256   the maintenance of cohesion and coordination.

257

As described above, we see that groups can differ widely in the way information is transferred to enable group coordination and decision-making, with simple cues sufficing under some circumstances, whereas evolved signals involving a variety of integration mechanisms are required in others. In the following sections we explore how communication used during group decision-making can be studied and compared across different social and ecological contexts.

Studying the role of ecological and individual heterogeneity in communication and collective decision-making

We predict a positive relationship between ecological heterogeneity (and the associated need for greater information transfer) and communication complexity surrounding decision-making contexts. In particular, species living in environments with greater ecological heterogeneity may need to utilize active signalling behaviours to coordinate their activities rather than rely on passive behavioural cues. For example, even though they share the same biome and sunbathe in the morning prior to foraging, meerkats produce activity-associated sunning calls that may control the timing of transition from sunning to foraging [98], while Cape ground squirrels (*Geosciurus inauris*) do not produce such vocalisations or any signal in other modalities (even though behavioural cues may still be used) [99]. Since Cape ground squirrels are central-place foragers and exploit the relatively simple environment nearby their burrow [100] while meerkats are multiple-place foragers and exploit various habitats throughout the day (e.g., open land, grassland, dunes…) [101], the greater communication complexity of meerkats during transitions between activities may be due to the increased ecological heterogeneity surrounding these decisions compared to Cape ground squirrels. Since meerkats and Cape ground squirrels differ in more than just their ecological complexity, a more rigorous test of the link between ecological heterogeneity and communication complexity would be to compare groups of the same species in environments of contrasting heterogeneity. As meerkat groups vary in their patterns of burrow usage [101], it could be fruitful to investigate whether groups with burrows further apart or groups that shift burrows more frequently use their sunning calls differently. Unfortunately, such studies are not yet available.

In addition to ecological heterogeneity, we predict that groups experiencing high conflict of interest due to high levels of individual heterogeneity may also need to use more complex communication systems (e.g., signals that better reflect individual states to coordinate their behaviours) when making collective decisions. Advertising motivational state is one way group members may flexibly gain leadership over group decisions made in these contexts, resulting in distributed leadership. For example, chimpanzees live in complex multi-male, multi-female fission-fusion societies, where group members may differ in both information about foraging preferences and information about available

292 food sources [102]. There is evidence that chimpanzee food-associated vocalizations share information
293 on the signaller's motivation to feed in a particular food patch, increasing behavioural coordination by
294 encouraging targeted group members to feed in this patch for a longer period of time and to remain
295 longer in the vicinity [84]. The flexible use of food-associated vocalizations may thus enable greater
296 influence over, or negotiation of, foraging behaviour among group members, potentially improving
297 coordination and decreasing social foraging costs. Comparing communication complexity across
298 foraging contexts when individuals are foraging in more or less heterogeneous subgroups could be one
299 way in which to test the predicted relationship between individual heterogeneity and communicative
300 complexity.

301 In another species, the greater spear-nosed bat (*Phyllostomus hastatus*), the use of food-associated
302 calls appears to be driven by ecological and individual heterogeneity simultaneously. Indeed, in one
303 population in Trinidad, balsa trees (*Ochroma pyramidale*) are located within 10 km of the roosting
304 caves and in different directions [103]. At another field site in Panama, the same species travel much
305 further (more than 20 km) in one particular direction to reach balsa trees and appear to travel and
306 forage alone (but within hearing range of other bats) [104]. Ecological and individual heterogeneity
307 therefore seems to be lower for the Panamanian population. Indeed, before reaching balsa trees, bats
308 from the Panamanian population have to fly over the ocean and large monoculture fields, which offer
309 little foraging resources, before reaching a single foraging patch (low ecological complexity) [104]. This
310 contrast with the higher diversity of foraging sites available around the cave for the Trinidadian
311 population (high ecological complexity) [103]. Additionally, in Panama, balsa trees are visited by much
312 larger animals, against which greater spear-nosed bats cannot compete (even in groups), providing no
313 benefit from foraging with conspecifics (i.e., low social complexity) [104]. However, in Trinidad, balsa
314 trees provide enough food for several individuals from the same group, in particular because group
315 members can efficiently defend access to this resource against other bat groups (i.e., supporting higher
316 social complexity) [103]. Even though it was not reported whether bats from the Panamanian
317 population produce screech calls while foraging, one could predict that, in this species, the relationship
318 between ecological heterogeneity, individual heterogeneity and communication complexity is
319 population dependent. Indeed, greater spear-nosed bats in Trinidad produce screech calls indicative
320 of the presence of food that attract group members (who can help in defending the resource) at a
321 specific location (among several around the cave) [103]. However, further studies should look into
322 whether and how bats from the Panamanian population use vocalizations in this foraging context.

323 As exemplified above, interspecies and intraspecies comparisons between animal populations are
324 required to understand the relationships between individual and ecological heterogeneity and
325 communication complexity. In particular, future studies should aim at comparing populations of the
326 same or similar species living in environments with varying levels of heterogeneity. Comparative work,

327 however, needs a consistent way to quantify heterogeneity and complexity. Employing a
328 multidimensional approach may be helpful for capturing key components of social, ecological, and
329 communicative complexity. In particular, Rebout et al. [31] have proposed a three-pronged approach
330 to measuring complexity that takes into account the diversity of elements in a system (e.g., the number
331 of categories of elements and how evenly elements are divided across categories), the flexibility of
332 these elements (i.e., the level of variability in individual elements) and the combinability of these
333 elements (i.e., how individual elements of a system can be combined into subunits) [31]. For example,
334 with regards to ecological heterogeneity, the ecological context within which collective decision-
335 making takes place can be more or less diverse (e.g., the number of relevant habitat types the decision
336 involves, as in the bat example above), more or less flexible (e.g., the temporal variability of habitat
337 types) and more or less combinatorial (e.g., how multiple habitat types may combine into broader
338 landscapes). Analogously, the social context during group decision-making can be more or less diverse
339 (e.g., the number and characteristics of individuals involved in the decision-making process, as in the
340 bat example above), more or less flexible (e.g., how temporally variable an individual's characteristics
341 can be - hunger level = high, age class = low) and more or less combinatorial (e.g., the effects of
342 coalitions or associations between multiple individuals).

343 The above approach can also be applied to communication complexity. For example, the use of
344 multiple call types (or individually distinctive call types) during a given group decision-making event
345 would represent an increase along the diversity dimension (e.g., the meerkat example above on
346 activity-associated vocalizations), the use of signals that reflect the signaller's changing motivational
347 state (e.g., the chimpanzee example above on food-associated vocalizations) would represent an
348 increase along the flexibility dimension, and the use of multimodal signals (signals integrating different
349 sensory modalities and encoding more information than single modality signals) [105,106] or of call
350 combinations would represent an increase along the combinability dimension, which can for instance
351 be used to resolve social uncertainty during fusion events [107]. Note that, in addition to
352 multimodality, the combinability dimension of communication can increase within each sensory
353 modality, by the use of syntax [108]. Finally, the mechanisms involved in integrating communication
354 signals can also differ along these three axes: the diversity dimension could refer to the number of
355 integration mechanisms used by a group during a given decision, the flexibility dimension could refer
356 to how these mechanisms can be used interchangeably, and the combinability dimension could refer
357 to how several integration mechanisms could interact. Generally speaking, this framework makes it
358 possible (i) to keep in mind that the heterogeneity or complexity of a system can vary along several
359 dimensions and (ii) to compare populations or species with different profiles on these various
360 dimensions. For example, in the context of specific collective decisions, such as group movements, this
361 framework makes it possible to compare species using numerous vocalisations (thus primarily the

362   diversity dimension) and species using different combinations of vocalisations (thus primarily the
363   combinability dimension).

364   Although general examples are provided above, this three-dimensional framework must be tailored to
365   knowledge of the collective decision-making event, and the species, under study. Specifying each
366   dimension and how to integrate them is beyond the scope of this paper, but examples exist for
367   measuring these dimensions for individual heterogeneity [31] and communication complexity [109] in
368   macaques. By calculating each of the three dimensions of complexity surrounding a given collective
369   decision-making context, they can be summed into a single, comprehensive measure of complexity for
370   the social context, the ecological context, and the communication behaviours involved [31]. By
371   repeating this process across different social groups of the same species, across the same social group
372   in different habitats, or across different species, the relationship between ecological, social, and
373   communicative complexity can be quantified for a given collective decision-making context.

374

375   **Leveraging new approaches to data collection, analysis and modelling**
376   The recent increase in the use of artificial intelligence and machine learning should eventually make it
377   possible to better assess the complexity of animal vocal communication in a standardized way,
378   particularly for the axes diversity and combinability. Several approaches already seem promising [110–
379   112], and are likely to be further refined as interested researchers become more familiar with these
380   techniques. For instance, vocal repertoires of over 10 species recorded in various settings can be
381   illustrated and compared using Uniform Manifold Approximation and Projection (UMAP), a
382   dimensionality reduction technique [112]. Similarly, artificial intelligence is increasingly applied to
383   measuring the ecological heterogeneity of an environment [113,114]. For instance, deep learning
384   algorithms can be deployed to assess which plant species are present on photographs, as well as their
385   abundance and their phenology state [115,116]. Concerning individual heterogeneity, more and more
386   algorithms are developed to automatically extract individual positions from videos (even without
387   markers attached to animals) [117,118] or to translate accelerometer data into underlying social
388   behaviours [119]. This high level of details is likely to render measures of ecological and individual
389   heterogeneities more dynamic and more fine-tuned.

390   Studies of the relationships between ecological and individual heterogeneity and communication
391   complexity can benefit from high-resolution tracking tools, particularly in the wild [120]. That is
392   because our predictions are specific to levels of ecological and individual heterogeneity and
393   communication complexity within given decision-making contexts, which must be tested using data on
394   a fine temporal scale (e.g., as opposed to examinations of repertoire-wide communication complexity
395   [121] or species-wide social complexity [122]). Studies leveraging wearable audio recorders, biologgers
396   [27,57] and algorithms able to reconstruct sensory social networks at high frequency (e.g., networks

397 that integrate the visual field of each individual to infer the social network of who can see whom at

398 each time step [123]) have begun to examine the role acoustic and visual signals play in the

399 coordination of group movement [27,57,124], as well as how they interact with the perceptual input

400 of each group member [123,125]. Furthermore, studies have examined relationships between group

401 coordination and decision-making and ecological heterogeneity by leveraging three-dimensional

402 habitat reconstruction [9]. By combining tools such as these, we can obtain detailed measurements of

403 ecological heterogeneity and communication complexity surrounding specific decision-making

404 contexts. For instance, Strandburg-Peshkin et al. [9] used basic categories of habitat type to investigate

405 the relationship between ecological heterogeneity and the cohesion of olive baboon troops (*Papio*

406 *anubis*) moving through their environment. In this field study, the baboons' environment was a mix of

407 'open,' 'medium,' and 'dense' habitats. The researchers found that medium habitats (which display

408 more heterogeneity than open or dense habitats) were associated with a wider range of group

409 structural configurations than either open or dense habitats. One could hypothesize that the

410 communication complexity used during collective decisions may also be different across these

411 habitats. For instance, we predict that the communication complexity involved in negotiating collective

412 movement would be higher (e.g., the use of individually-distinctive calls or multimodal signals) in

413 medium (more heterogeneous) habitats than in open or dense habitats. By combining data loggers

414 with 3D environmental imaging, these predictions could be directly tested.

415 In the same way that these new technologies allow for easier acquisition of large amounts of high-

416 resolution data, they can also allow for more controlled experimental approaches. For example,

417 proximity sensors between individuals in a group and elements in their environment (bushes, water

418 points...) could be used to allow or deny access to these environmental elements (thus allowing or

419 denying access to resources to different group members). Such approaches could be used to test the

420 relationship between the newly manipulated individual heterogeneity and the complexity of

421 communication signals used for associated collective decision-making. For example, studies have

422 found that capuchins produce "trill" vocalizations when traveling on the edge of the troop which

423 correlate with subsequent changes in direction by the troop in the direction in which the signaller(s)

424 were traveling [126]. Such call production may provide group members with greater control over group

425 travel direction in cases where movement direction preferences diverge. Comparing communication

426 complexity across contexts in which individual travel preferences are more or less heterogeneous (e.g.,

427 through an experimental food patch that provides access to some or all group members) could be one

428 means to test the predicted relationship between individual heterogeneity (and associated conflicts of

429 interest) and communication complexity. Such technologies will likely render experiments more

430 dynamic and more contextualized and therefore increase their ecological validity. Even though still in

431 its infancy, another technique that could be employed to better control the social and ecological

432   environments in which group members make collective decisions is the use of virtual reality [127]. In

433   this way, the perceived heterogeneity of the environment could be directly manipulated, enabling

434   experimental tests of its impact on communication complexity.

435   Finally, agent-based modelling and other forms of computational modelling can help to determine

436   whether simplified behavioural rules can replicate observed collective decision-making. For example,

437   in an agent-based model, Sellers et al. [128] determined which factors were most influential to produce

438   collective movements most similar to observed patterns, while requiring the agents to fulfil their

439   individual needs (eating, drinking, sleeping and social activities) as much as possible. They found that

440   the variable most important for the model to succeed or fail was the proportion of agents required to

441   vote before the group moves (i.e., a quorum). In contrast, models of collective departure in goats

442   enabled the determination that goats do not vote on their preferred direction of travel using their

443   body orientations but rather begin to move in a given direction by simply following the movements of

444   their neighbours [57]. Using such approaches can clarify the behavioural mechanisms underlying

445   collective decision-making while also promoting comparison of the mechanisms for information

446   transfer and communication across species and contexts [129]. For example, recent modelling

447   approaches have been used to determine which communication types are more efficient in specific

448   socio-ecological contexts. For instance, in pairs of homogeneous individuals foraging in patchy

449   environments, pulsative communication (i.e., signals produced by individuals only once their decision

450   is made) is more efficient than diffusive communication (i.e., signals produced throughout the

451   deliberation phase) to coordinate patch departure decisions [87]. However, diffusive communication,

452   which may be more complex to produce and/or integrate at the group level, could be more efficient

453   in larger groups, as diffusive communication dampens increased noise that is bound to occur in larger

454   groups [87]. Which communication type is better suited for less patchy environments or with larger

455   interindividual heterogeneity within groups remain open questions [87]. Another modelling approach

456   that shows great potential to explain social foraging derives from the classic Marginal Value Theorem

457   [130,131]. Individual-level foraging data can be used to determine the optimal patch departure time

458   for each group member and to calculate associated consensus costs [130]. It would be rewarding to

459   combine this framework with data on communication in order to determine whether the complexity

460   of communication produced in foraging contexts is more complex when group members have more

461   divergent (i.e., heterogeneous) preferred departure times.

462   All together, these exciting measurement, experimental and modelling approaches will bring

463   unprecedented developments to our understanding of how group members in specific socio-ecological

464   contexts leverage communication signals to make group decisions, particularly when making

465   comparisons both within and between populations and/or species [132]. In this way researchers can

466 test if the themes addressed in this perspective are applicable to other social systems (e.g.,

467 Hymenoptera, birds) and environments (e.g., marine) which we have focused less on here [133–136].

468

469 **Conclusion**

470 We highlight the key role communication can play in collective decision-making and propose that a

471 maximal increase in communication complexity in such contexts occurs when both ecological and

472 social pressures demand it. We predict that a positive relationship between communication

473 complexity and individual and ecological heterogeneity enables individuals to successfully navigate

474 their ecological and social puzzle during collective decision-making contexts. In this way, species can

475 reach collective decisions within ecological and social niches of increasing heterogeneity.

476

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480

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