Using optimal foraging theory to infer how groups make collective decisions

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Abstract
Studying animal behavior as collective phenomena is a powerful tool for understanding social processes, including group coordination and decision-making. However, linking individual behavior during group decision-making to the preferences underlying those actions poses a considerable challenge. Optimal foraging theory, and specifically the marginal value theorem (MVT), can provide predictions about individual preferences, against which the behavior of groups can be compared under different models of influence. A major strength of formally linking optimal foraging theory to collective behavior is that it generates predictions that can easily be tested under field conditions. This opens the door to studying group decision-making in a range of species; a necessary step for revealing the ecological drivers and evolutionary consequences of collective decision-making.

Optimal foraging theory and collective animal behavior

Collective behaviors are remarkable natural phenomena in social organisms, and how interactions between individuals produce emergent patterns of behavior has received considerable attention[1–5]. A central question in the study of collective behavior is how individuals in groups coordinate their behavior and reach (or fail to reach) consensus decisions (see Glossary) about where to go, when to move, and what to do[6–11]. However, a key challenge to studying how such decisions are made in wild animals is the difficulty of establishing the link between individual preferences and the resulting collective outcome(s). While the outcomes of consensus decisions can be documented[12–16], determining the processes by which decisions are made requires the ability to predict, and empirically assess, the preferences of each group member[17].

The strong theoretical basis that exists for studying individual foraging decisions provides a rare opportunity to elucidate the dynamics of collective decision-making. In particular, the existence of clear and measurable currencies – energy and time – facilitates comparison of individual preferences and decision outcomes across collective foraging scenarios. Optimal foraging theory[18,19] can predict animals’ decisions, including diet choice[20,21], where to eat[22], and how to move between resources[23,24]. The marginal value theorem (MVT)[25], for example, can be used to predict when individuals should leave a resource patch based on their current intake rate and the distribution of resources in the landscape (Box 1). A rich body of theory[26–31] and empirical work[32–38] have explored such foraging decisions within aggregations of individuals. However, in animals that form cohesive groups with stable membership, decisions are socially contingent[32–34]. For example, costs and benefits of foraging decisions can differ among group-mates[12,39], and different-sized groups can vary in how rapidly they exploit patches[27,40]. Formulating the MVT for cohesive social groups – whereby individuals all leave patches together – can reveal the conflicting preferences between group members, how groups make decisions (i.e., who has influence), and the costs that individuals pay to achieve consensus.

Highlights

A growing body of evidence emerging from the analysis of advanced animal tracking data shows that moving groups make shared decisions about where to go, with each group member influencing the outcome. How groups coordinate departure decisions (when to go), however, remains poorly understood.

Classic models from optimal foraging theory, specifically the marginal value theorem (MVT), are well-established tools that can generate quantitative predictions about how individuals should prefer to leave a food patch, given patch quality and the distribution of patches in the environment.

Integrating optimal foraging theory into studies of animal collectives provides rich opportunities for gaining new insights from both empirical and theoretical studies. Specifically, the MVT can be used to make predictions about conflict of interests among group members, how consensus costs vary under different models of collective decision-making, and under what environmental conditions shared decision-making may be favored or disfavored.

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Box 1: Optimal foraging theory

Optimal foraging theory predicts the outcome of individual foraging decisions when resources are temporally variable. Optimal foraging theory is based on the marginal value theorem (MVT), which is the notion that an individual should continue foraging when the gain from the next unit of foraging exceeds the opportunity cost of forgoing the next unit of foraging. The MVT is a simple, yet powerful, tool that has been widely used to predict the outcome of individual foraging decisions. However, the MVT is a static model and does not account for the dynamic nature of foraging decisions. To address this limitation, dynamic models have been developed, which take into account the temporal variability of resources. Dynamic models have been used to predict the outcome of individual foraging decisions under a wide range of conditions, including those in which resources are spatially variable. Dynamic models have also been used to predict the outcome of collective foraging decisions, which are decision-making processes in groups of animals. The MVT is a useful tool for understanding the outcome of individual and collective foraging decisions, and it is widely used in ecology and behavioral ecology. However, the MVT is a static model and it does not account for the dynamic nature of foraging decisions. To address this limitation, dynamic models have been developed, which take into account the temporal variability of resources. Dynamic models have been used to predict the outcome of individual foraging decisions under a wide range of conditions, including those in which resources are spatially variable. Dynamic models have also been used to predict the outcome of collective foraging decisions, which are decision-making processes in groups of animals.
Here, we lay out a framework for integrating optimal foraging theory – specifically the MVT – into studies of collective decision-making of cohesive groups with stable membership. We show that making consensus decisions results in consensus costs, and that the MVT can combine empirical data on rates of prey acquisition (to estimate individuals’ gain curves) together with the observed group departure time to infer who has influence and how groups make decisions.

Applications of the marginal value theorem to cohesive social groups

Beyond deciding where and how to search for food [41,42], foragers must also decide how long to feed on one resource patch before leaving to find a new patch. The MVT predicts that these decisions should be based on the instantaneous rate of energy gain. As an animal starts to deplete a patch, the rate at which energy is gained decreases, reaching a point where it is more profitable to search for a new food source than to remain. Foragers are therefore expected to leave when their current rate of energy gain falls below the average rate of energy gain for the habitat (their optimal patch departure time) [25]. Although the MVT is an over-simplification of animals’ decision-making processes [43,44], its predictions nonetheless continue to be supported across a diverse set of organisms (e.g., birds, [45,46]; hunter-gatherers, [38,47]; non-human primates, [35,48]; rodents, [49]; insects, [33]). These studies also demonstrate how the MVT can be tested using field data. Specifically, the number of prey items individuals consume per unit time can then be fitted with negative exponential models, from which their optimal departure times can be estimated.

Box 1. Basic social patch exploitation models

The gain curve of a forager in a patch, as a function of the time since entering the patch (t), can be modeled as a negative exponential function:

\[ W(t) = 1 - \exp(-\mu t) \]

where the cumulative energy gained by an individual over time (\(W(t)\)) increases faster as a function of harvest rate (\(\mu\)), but has an exponentially decreasing rate leading to an asymptote. An individual is expected to leave a foraging patch when its current rate of food capture falls below the average capture rate for the habitat [25], which is given by the point maximizing \(\frac{\mu}{\lambda}\), with \(\mu\) being the average travel time between patches. However, some prey items require handling time (\(h\)), reducing the rate of energy gain. In such cases, the time taken to extract the gth prey item from a patch containing G prey items (the inverse of the gain curve) is given as [99]:

\[ t(g) = \frac{1}{\lambda} \log \left( \frac{G}{G - g} \right) + hg. \]

The simplest extension of the solitary patch model to social groups considers depletable patches that are exploited by N foragers that arrive and leave the patch simultaneously. The model [28]:

\[ W(N) = 1 - \exp(-\lambda N t) \]

assumes that all group members have the same instantaneous patch exploitation rate. It predicts that all individuals should have the same patch residency time, which is equal to the group-level optimal patch residency time (\(T_G = T_i\)). The MVT generally predicts that individuals should live in small rather than large groups because the per capita energy gain over time (\(\frac{\mu}{\lambda} + \frac{h}{\lambda}\)) is typically greater in smaller groups. However, if larger group size enables greater individual harvest rates (\(\lambda_i\)), for example, due to reduced vigilance or enhanced group performance [40], then the foraging favors larger groups, but only if the travel time between patches is short (not shown). If travel time is also affected by group size (e.g., larger groups move more slowly [100]), this could yield an optimal group size for optimal foraging.

The MVT further predicts that (larger) groups should leave patches sooner (due to more foragers encountering and consuming prey items) and deplete resources to a greater extent (due to having a higher overall harvest rate), than individuals (Figure B) or smaller groups (Figure C). Food items that involve handling time reduce the per capita intake rate, leading to greater patch residency times. This has a stronger impact on individuals living in large (Figure D) versus small groups (Figure E).
The MVT can be readily extended to social foraging contexts where animals travel and exploit resources as groups. These include troops of primates [50–53]; bird flocks, including old world babblers (Family Timaliidae) [54,55], cooperative breeders (e.g., superb fairy-wrens Malurus cyaneus [56], white-winged choughs Corcorax melanorhamphos [57]), family groups (e.g., black-capped chickadees Poecile atricapillus [58]), and species forming multilevel bird societies (e.g., vulturine guineafowl Acryllium vulturinum [59]); stable groups of bats (e.g., Spix’s disk-winged bat Thyroptera tricolor [60]); cetacean pods [61]; and mongoose groups [62,63]. Whether highly cohesive or more distributed (the MVT is scale insensitive), group daily movements extend much farther than their spread, with members switching from local foraging movements to directed movement. Thus, to effectively exploit foraging resources across their range — inerctucescences, schools of bait fish, open grassy areas, masting trees — group members must coordinate their activities and reach consensus over not only where to move [12,14,64], but also when to move [65].

While several social formulations of the MVT exist [28,66], these assume group members are identical. They predict that all group members share the same optimal patch departure time, also matching the optimal departure time given by the group-level gain curve (the sum of all the individual gain curves; see Figure IA in Box 1). Current social implementations (Box 1) already highlight tradeoffs arising from foraging as (larger) groups versus foraging alone or in smaller groups, and how tradeoffs are impacted by the distribution of patches across the environment, the types of food available within patches, and the foraging performance of groups. Thus, even in its simplest forms, the MVT already makes useful predictions when applied to social groups.
Predicting conflicts of interest over when to leave

When applied to stable social groups, the MVT can capture variation between group members in their foraging behavior and ultimately their preferences over when to leave a patch. In most species, groups contain individuals that differ in size, dominance status, experience, and abilities [67–69]. Such characteristics can correspond to differences in abilities at extracting resources from the environment (e.g., intake rates, processing times), distinct gain curves, and therefore, within-group differences in optimal patch departure times. Thus, collective departures (the observed group departure time) will deviate from the optimal departure time of some group members, introducing opportunity costs relative to lone foraging [65]. Here, we show that extending the MVT to such group-foraging contexts is relatively straightforward (Box 2), and provides a way to predict, and quantify, conflicts of interest over the timing of group departures.

In heterogeneous groups that move together, group members will differ in their ability to extract energy from the patch, as well as the total quantity obtained. Such differences can alter the environment experienced by different group members, thereby introducing variation in the rate of energy gain. Unequal access to the patch alone will not generate conflict over the timing of movements, as the MVT predicts that otherwise identical individuals will have the same optimal patch departure times despite interindividual differences in overall energy gain (see Figure IA in Box 2). However, if resources are heterogeneously distributed in the patch, individuals with access to better parts of the patch (e.g., dominants [12,70–72]) experience a richer environment than those relegated to the poorer parts, generating within-group variation in optimal patch departure times. Specifically, individuals with a higher harvest rate are predicted to have earlier optimal patch departure times than other group members (see Figure IB in Box 2). Foragers also vary in their ability to process and consume prey. For instance, individuals can become more proficient at handling food items as they accumulate experience [73–75]. The MVT predicts that longer handling times lead to later optimal patch departure times (see Figure IC in Box 2). Thus, unequal access to the best foraging sites and variation in foraging ability, but not differences in the total amount of energy extracted from a patch, will introduce conflicts of interest within groups over the timing of departures.

Individuals can simultaneously differ across multiple dimensions, such as experience, dominance, and personality, leading to some unexpected, and perhaps counterintuitive, predictions. For example, scenarios exist where better foragers are predicted to have later optimal departure times (e.g., see Figure IE in Box 2). Such predictions illustrate the value of formal modeling for generating predictions about the conflicts of interest that arise in groups of heterogeneous foragers, including species that do not maintain strictly cohesive groups with stable membership but that benefit from collective behaviors, with individuals balancing the need to depart with the risk of moving alone (e.g., leaving before the group, or remaining after the group leaves).

Testing how groups resolve conflicts of interest to reach consensus

Taking research on leadership and influence in animal groups out of the laboratory and into ecologically, socially, and evolutionarily relevant field settings has proven remarkably challenging [76]. While aided by technological advances [3], studies focusing on observations of movement initiations (attempts to lead the group away from a patch) have not been able to directly link individuals’ contributions to group decisions to the preferences underlying their actions [12,14,77–79] (but see [15]). Optimal foraging theory can provide a deeper mechanistic understanding of how group-living animals resolve conflicts of interest.

One challenge for studies of collective decision-making is to identify who has influence [17]. By comparing observed group departure times with the predicted optimal departure times of...
Box 2. Heterogeneity in groups can generate conflicts in optimal patch departure times

When groups have heterogeneous membership, differences in gain curves among group-mates can lead to conflicts of interest over the timing of patch departures (i.e., differences in the predicted optimal departure time among group members). Only when individuals vary solely in the total amount of energy they can extract from the patch (the asymptote of their gain curve, where \( W(t) = 0 \)) will all individuals have the same optimal departure time as each other and as the group (Figure A). If individuals differ in their harvest rate (\( \lambda \) varies), those with a higher \( \lambda \) can extract their share of the energy from the patch faster, and are predicted to have an earlier optimal patch departure time than individuals with a lower \( \lambda \) (Figure B). More efficient individuals also extract more energy from the patch at their optimal departure time than less efficient individuals. Individuals can also vary in their handling time for each prey item. In this scenario, individuals with shorter handling times are predicted to have earlier optimal departure times than individuals with longer handling times, but all individuals will acquire the same energy at their optimal departure times (Figure C).

In natural populations, individuals often vary across several parameters simultaneously. Individuals that obtain a greater portion of the total energy and harvest resources faster can have longer optimal patch residency times (Figure D), as do those gaining a greater portion of total energy with shorter handling times (Figure E). However, having a greater harvest rate and shorter handling times (Figure F) lead to earlier optimal departure.

Figure I. Interindividual differences in foraging behavior can lead to variation in the shape of the energy gain curves for group-foraging animals, and thus differences in optimal patch departure times of group-mates. (A–F) Six examples of how individuals can differ in their foraging strategies and abilities, resulting in conflicting departure times. The top black unbroken gain curve in each image represents the cumulative energy acquired by the group as a whole (N = 3). The lower colored broken gain curves are the cumulative energy acquired by each group member. Dotted lines capture the optimal patch departure times for each individual (\( T_1 - T_3 \)) and for the group as a whole (\( T_G \), diamonds). Squares represent the mean of the group members’ optimal departure times (if not shown, this equals \( T_G \)). Individuals can vary in: (A) the total amount energy they can extract from the patch, (B) harvest rate, (C) handling time, (D) the total amount energy they can extract from the patch and harvest rate, (E) the total amount energy they can extract from the patch and handling time, and (F) harvest rate and handling time. In all cases, individual 1 (blue line) has the “best” parameters (highest energy gain, greatest efficiency, and shortest handling time), followed by individuals 2 (yellow broken line) and 3 (gray broken line).

Group members, the MVT can reveal influence without making assumptions about mechanisms. Influential individuals (e.g., despots) could be identified by a tendency for their group to leave foraging patches at or close to their optimal departure time (Box 3, \( D_0 \), where \( T_1 \) is a despot) as opposed to the group-level optimum (\( T_G \)) or the optimal departure times of other group members (\( T_2, T_3 \)). Decisions that are shared equally across group members are expected to have a departure time matching the average time for all, which groups might approximate as the time when a majority (or sub-majority) of individuals have reached their optimal departure times (\( D_0 \)). This approach avoids relying on observations of initiators, potentially revealing the long-hypothesized role of followers on the timing of departures [80].
Comparing when groups depart to predictions from the MVT can then be used to quantify individual consensus costs [10]. Consensus costs can be measured in terms of the energetic (foraging) loss as a result of leaving either earlier or later than the predicted optimal patch departure time for each individual (an opportunity cost, Figure 1A) [65]. Consensus costs can also be estimated under different decision-making processes, and can be used in a range of analyses, including comparative and evolutionary studies.

**Box 3. Using optimal foraging theory to reveal collective decision-making processes**

By comparing the discrepancy between individual optimal departure times \(T_1, \ldots, T_N\) versus the group’s observed departure time from the patch \(D\), we can understand how groups of individuals come to decisions about when to leave, and who exerts the most influence. We use the MVT to predict when groups should leave patches under three common collective decision-making situations: shared (or quorum-based) decisions \(D_S\), despotic decisions \(D_D\), and globally optimal decisions \(D_G\).

When decisions are shared, all (or a representative proportion) of the group contributes to the group-level decision. Shared decisions are often represented by a fixed threshold or a quorum (a probabilistic threshold of group members or a ‘majority rule’). In the context of social foraging, we predict that groups will leave food patches once a certain number of individuals in the group (or the median individual given a majority rule) have met their optimal patch departure times (Figure 1, \(D_S = T_2\)).

In very large groups, the median of all individuals’ departure times will be closely aligned with the group-level optimal departure time, highlighting a potential selective driver for shared decision-making.

At the opposite end of the decision-making spectrum [96] are despotic, or unshared, decisions. In a foraging context, a single individual has sole influence over the group decision about when to leave a foraging patch, and the observed departure of the group is predicted to align with the predicted optimal departure time of the despot (Figure 1, \(D_D = T_1\)).

Finally, individual-level energy gain could potentially be optimized by departing at the optimal departure time based on the overall group gain function (Figure 1, \(D_G = T_G\)). For example, if individuals vary unpredictably in their harvest rates from one patch to the next, then their individual-level energy gain over multiple patches could be maximized if they depart at the group-level optimal departure time. Thus, taking an optimal foraging view of collective decision-making reveals an alternative mechanism for reaching decisions that have not been previously considered.

Under both shared or despotic mechanisms, the group departure time can be either earlier or later than the group-level optimal departure time, which could have implications for the group’s performance relative to other groups in the same habitat (e.g., if they exploit fewer resources relative to their travel time). Exploring the relative group-level gains under different levels of individual variation (Box 2), in groups with different decision-making mechanisms, and across different habitats (Figure 1) in a selection framework will yield novel insights into what type of decision-making mechanisms should evolve.

**Figure 1. Conflicts of interest about optimal departure times can arise as a function of individual variation, such as when individuals differ in their (A) harvest rate or (B) total energy gain and harvest rate. Here, we demonstrate how conflicts can lead to different predictions about when groups should leave under three models of group decision-making: shared \(D_S\), despotic \(D_D\), and group optimal \(D_G\). Diamonds represent the group-level optimal departure time \(T_G\).**

Comparing when groups depart to predictions from the MVT can then be used to quantify individual consensus costs [10]. Consensus costs can be measured in terms of the energetic (foraging) loss as a result of leaving either earlier or later than the predicted optimal patch departure time for each individual (an opportunity cost, Figure 1A) [65]. Consensus costs can also be estimated under different decision-making processes, and can be used in a range of analyses, including comparative and evolutionary studies.
Ecological drivers and evolutionary implications of collective departures

Consensus costs are a central mechanism underpinning the social structure of animal social groups [81], and animals can respond to changes in the magnitude of consensus costs by modifying the structure of their societies [82]. For example, if compromise is too costly for individuals (relative to the benefits of remaining in a group), then fission–fusion dynamics emerge in lieu of consensus decision-making [83]. The magnitude of the costs borne by individuals (or the total cost experienced by a group) may be shaped by the environment itself—specifically the travel time between patches. Consider the simplest case where individuals vary in their harvest rates (λ; see Figure 1B in Box 2), causing a spread in the optimal foraging times of group members (T1...TN). The size of this spread will not only be dictated by the variation in harvest rates, but also by the travel time. At very short travel times, the energy intake rate trajectories among individuals have had little opportunity to diverge before they should each choose to move on, yielding a small variation in optimal departure times. Similarly, as travel times become very long, all individuals should exploit as much of the patch as possible, causing the energy intake trajectories to converge. Thus, at intermediate travel times, individuals experience the greatest spread in their energy acquisition curves, resulting in more divergent optimal departure times.

Examining the relationship between ecological conditions (variation in travel time) and the resulting consensus costs that emerge from individuals diverging from their optimal departure times (Figure 1B) confirms that group-level consensus costs are minimized in both resource-rich (shorter travel times between patches) and resource-poor (longer travel times between patches [68]) environments, and maximized in environments with intermediate resource availability (Figure 1B). This suggests that maintaining social cohesion entails increasing costs when transitioning from high-quality environments, but that these costs shrink again as conditions become even less favorable. By predicting a decrease in consensus costs in environments when conditions become harsher, the MVT might therefore help to explain the apparent paradox that environmental harshness (low rainfall combined with seasonal unpredictability that increase travel time as groups forage over larger areas [56,84]) can result in greater social cohesiveness, such as in the evolution of cooperation [85,86] or the fusion of groups within mammalian and avian
multilevel societies [59,87–91]. This demonstrates how integrating the MVT with models of collective decision-making and collective movement has significant potential to generate predictions about the evolution of group-living under different ecological conditions.

A final question is whether cohesive groups can maximize the rate of energy extracted from the environment by leaving patches at the optimal time predicted by the group-level gain curve (Boxes 1–3, T₂). This could be beneficial if, for example, the group member(s) that access better parts of a patch varies (unpredictably) from one patch to the next as it maximizes the average rate of harvest from the environment across group members. Several examples demonstrate how collectives can produce such higher-level optimization. One classic example is the ideal free distribution [92], whereby individuals maximize their fitness by spreading themselves across heterogeneous resources in such a way that maximizes their individual harvest rates, thereby also maximizing the harvest rate of the group or population. Thus, animals could have evolved fine-tuned collective decision-making mechanisms that benefit them via optimal performance of their group (see Outstanding questions).

Finally, two intriguing predictions of the MVT are that the mean of the departure times across group members can be equal to, earlier, or later than the group-level optimal departure time (Box 2), and that the predicted optimal departure time for a given group does not always match the optimal departure time based on a majority-based decision (i.e., T₂ ≠ T₃ in Box 3). Future studies could investigate the consequences of these mismatches. For example, if individual optimal departure times are long-tailed, then decisions could be made by a sub-majority [10]. Such sub-majority decisions were observed in group-living vulturine guineafowl, where subordinates that are displaced from patches initiate movements away on reaching ~13 individuals, irrespective of group size [12] (which can range from 15 to 65 [59]).

Using the marginal value theorem in empirical studies of collective decision-making

Group decision-making processes can be inferred by collecting foraging data from group members, estimating harvest rates and how these change over time, and observing group departure times. There are many ways to collect foraging data, including recording intake rates for all group members in the patch concurrently using observations or video recordings (e.g., [12]), collecting short repeated foraging observations from group members asynchronously (e.g., [35]), or focusing on two group members at once to quantify conflicts of interest dyadically (e.g., between a dominant and a subordinate). Two potentially useful ways to facilitate observational data collection are to create experimental patches where the amount of food is known a priori [49] or to estimate foraging return rates by weighing food items acquired by group members [38]. Foraging time could also be inferred from behavioral classification of biologging data, such as detecting prey encounters from accelerometer data [93] or detecting chewing from microphones [94]. Importantly, all of these approaches can allow data collection across repeated foraging patches (see Outstanding questions).

From the foraging data, individual harvest rates (and how these change over time) can be modeled by fitting negative exponential models. Models allow individual gain curves to be extended beyond when they leave the patch to calculate the theoretical individual-level optimal departure times. This calculation is done by combining gain curves with data on travel time, which is readily available in studies that follow groups while collecting global positioning signal (GPS) data (e.g., [51,88]) or in the increasing number of studies that fit GPS loggers to at least one group member (e.g., [12,14]). Finally, the energetic consensus cost can be calculated for each individual as the difference between the actual rate of energy gained relative to the theoretical maximum.
energy the individual could have extracted from the environment had it left at its optimal departure time (per Figure 1A). These four simple steps—obtaining foraging data over time, fitting individual-level curves, estimating individual-level optimal departure times, and calculating consensus costs—are readily achievable in most field systems.

Concluding remarks
Despite a wealth of theoretical models of collective decision-making in animals [9,83,95–98], few empirical studies have moved beyond asking ‘who leads’ to explicitly testing how groups make decisions [17]. This is largely because determining how consensus decisions are reached in natural systems is significantly more challenging than observing the decision outcomes (i.e., where or when groups move). We highlighted that the MVT helps us understand collective decision-making by: (i) predicting when each individual should want to leave a patch, (ii) quantifying conflicts of interest for any given decision, (iii) precisely predicting when groups should depart a patch under different models of collective decision-making, (iv) quantifying consensus costs in ecologically meaningful currencies (energy, time) and identifying who pays them, and (v) predicting when ecological conditions stable groups should pay greater versus fewer costs. In doing so, the MVT will help the field of collective behavior become a more predictive science by providing predictions that can readily be tested under field conditions. Further, while we have focused on animals that form cohesive groups with stable membership, the model is also applicable to open societies, where animals forage socially but vary in when they access patches and must decide whether to optimize their departures to maintain cohesion or maximize energy gain. Finally, the MVT and other models from optimal foraging theory can readily be integrated into evolutionary models of collective decision-making, potentially providing a rich framework for studying the evolution of collective decision-making under different social (e.g., group size, competitive regimes, and composition) and ecological (e.g., habitat type or predation risk) conditions (see Outstanding questions).

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Outstanding questions

Broader contexts
Can optimal foraging models inform other aspects of group decision-making, such as where to go next or what resources to favor?

How do consensus costs and within-patch competitive dynamics among group members impact the foraging strategies used by individuals (e.g., whether they are generalist foragers or specialist foragers in heterogeneous patches, or whether they invest in learning how to better handle prey items)? Such questions could be addressed by applying a game-theoretic approach to optimal foraging theory, which can better integrate frequency-dependent processes that arise when group members compete for prey items.

Repeated decisions
Do departures matching the group’s optimal departure time also maximize individual performance over repeated foraging events, given other processes such as satiation or accessing patches with different food types?

How are consensus costs accumulated or averaged over the course of sequential decisions?

Consensus costs
How does within-group variation in patch quality experienced by individuals over sequential patches (e.g., stochasticity in which individuals access better parts of patches) shape the evolution of decision-making processes?

How does asynchrony in access to the patch affect consensus costs? Does waiting for access to patches or while initiating departures from patches reduce conflicts among group members, for example, by delaying initiators’ optimal departure time as a result of increasing their inter-patch access time (waiting plus travel times)?

When do the mean of group members’ optimal departure times differ from the group-level optimal departure time?
What is the magnitude of the consensus costs – in terms of foraging efficiency – of living in a group?

How do different axes of individual variation in foraging (e.g., personality, producer-scrounger roles, foraging abilities) impact conflicts of interest within a group?

Ecological implications

Do groups change how they make collective decisions to optimize departure times, or minimize consensus costs, under different environmental conditions?

How does predation risk affect consensus costs, given differences in risk and predator detection across group sizes, and does the effect of predation on collective decisions vary depending on whether risk is greater in patches or when traveling between patches? In the case of predation risk within patches, it should increase vigilance and reduce the harvest rate. In the case of predation risk between patches, it should favor strategies that minimize the proportion of time individuals (and groups) spend moving between patches (e.g., by delaying group departures).
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