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Research Article

Optimal foraging can drive emergent initiator-follower dynamics in social groups

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Deciding when and where to move is a challenge for group-living animals as differences in preferences must be resolved for the group to maintain cohesion. In many species, consensus is reached through shared decision-making, whereby group members initiate group movements by stopping foraging and making directed movements away from a feeding source. Yet, despite being widespread, it is unclear how this initiation process has emerged in animal groups, and theory has yet to resolve the paradox of why some individuals forego foraging to instigate collective movements. By applying theoretical predictions from the marginal value theorem to heterogeneous foraging groups, we show that 1) movement initiations can reduce subsequent within-group conflict over when to depart, 2) habitat heterogeneity and within-group differences in foraging rate shape who initiates, and 3) different forms of collective decision-making can emerge under different environmental conditions. These results demonstrate that optimal foraging theory can resolve outstanding questions about leadership in collective movements of animal groups.

Keywords: collective behaviour, collective decision-making, group-living, leadership, marginal value theorem, social behaviour

Introduction

'*If a bird of either sex moves off in a determined manner, the whole covey may follow. [..] If a pioneering bird is not followed by others it abandons its exploring and hurries back to rejoin the covey*' Leopold (1977) p. 68 describing movement initiations in California quail *Callipepla californica*.

Animals are time limited, driving behavioral adaptations to optimise efficiency (Dunbar et al. 2009). For example, when actively foraging – finding and exploiting food resources – individuals should aim to maximise their rate of intake to ensure that they acquire the necessary energy, with this time being traded off against other

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necessary maintenance activities (e.g. scanning for predators, social interactions, resting). This challenge is exacerbated for group-living animals that maintain high levels of cohesion – including many primates, small mammals and birds – because group members may differ in their preferences for which activity to engage in at any given time (Davis et al. 2022). When faced with such conflicts of interest over when to depart, one strategy is for groups to split (Conradt and Roper 2007, Sueur et al. 2011); but in many species, groups instead maintain cohesion, making consensus decisions to depart, travel and enter new patches together. The need to resolve conflicts of interest within such groups is likely to have been a key driver behind the evolution of shared decision-making (Couzin and Krause 2003, Conradt and Roper 2005, Biro et al. 2006, 2007, 2009, Ogino et al. 2023). Shared decisions are those where any group member can (but does not necessarily have to) contribute to deciding what action the group should do next. One way that differences in movement preferences among individuals can be communicated and resolved is through movement initiation attempts.

Movement initiations are common across a range of taxa (Harcourt et al. 2009, Petit and Bon 2010, Jacobs et al. 2011a, Pyritz et al. 2013, Ramos et al. 2015, Wang et al. 2020). An initiator is typically defined as an individual that moves away from the current location of its group, usually in its intended direction of travel, and waits for other group members to follow (and returns to the group if they are not followed) (Strandburg-Peshkin et al. 2018). Such movements are often stereotypical to make them more salient (Liao et al. 2024), and thus act as a source of information to other group members (Valone 1993, Valone and Giraldeau 1993). While initiations have been well-studied in the context of determining how groups make directional decisions (e.g. groups may move in the direction that contains the majority of initiators) (Conradt and Roper 2003), our understanding of how collectives make timing decisions (and the role of initiations therein) remains limited (Kao et al. 2024). For example, an individual could initiate movement when it is ready to leave a foraging patch and search for a new one, with the group eventually departing when sufficient group members have initiated movements (as shared decisions do not require all group members to be involved in every decision). A key factor is that when making such an initiation attempt, the individual also generally foregoes (or significantly reduces) foraging (Papageorgiou and Farine 2020, Ramos et al. 2015), while also not actively traveling towards new patches, thereby introducing a wait time (ω). Shared decision-making can thus turn collective departure decisions into protracted affairs (Gavrilets et al. 2016) that will have an impact on the time budget of the initiators and the efficiency of group members (Klarevas-Irby et al. 2025). Making an initiation attempt would therefore only be worthwhile if it can either increase its future foraging rate (to offset the time spent waiting) or if it reduces conflicts among group members. However, to date there has not been a framework that has looked at whether we can predict which individuals make movement initiations, when they do so, and if there are consequences of these at the group level.

One classical framework for understanding how time and energy are linked (through foraging rate and movements) is optimal foraging theory. Specifically, the marginal value theorem (MVT) predicts that the optimal time for individual foragers to leave a food patch is when their current food intake rate $g'(t)$, which decreases the longer they remain in a patch, drops below the average (background) intake rate that they have experienced while foraging in the environment $g(t)/(\mu + t)$ (the total energy gained divided by the sum of the foraging and travel times; Charnov 1976). Individuals that leave a resource patch earlier than their optimal time, as predicted by the MVT, pay a foraging cost by abandoning the patch while they were still accumulating food at a higher-than-average rate. By contrast, those that leave later than their optimum pay an opportunity cost by missing out on better foraging opportunities elsewhere. The MVT also makes useful predictions about how long solitary foragers should spend in a food patch under different environmental conditions (Calcagno et al. 2014). In poorer environments – where individuals have lower foraging efficiency (λ), for example because a lower food abundance, increased predator pressure elevating scanning rates, and/or longer travel times between patches (μ) reduces their average intake rate – the MVT predicts that individuals should remain in patches for longer. In richer environments – where the average food intake $g(t)$ is faster due to higher foraging efficiency or shorter travel times – solitary foragers should depart food resources sooner. Thus, foraging efficiency and habitat quality together shape the timing of departure decisions made by individual foragers.

A key factor is that in social animals, individual group members often vary in their ability to compete for, acquire, and process food. Such variation in foraging abilities can arise from differences in, for example, age, sex, experience, size and other traits. For instance, it has been widely reported (Parker and Sutherland 1986, Bautista et al. 1995, Holmgren 1995, Tregenza et al. 1996, van der Meer 1997) that dominant individuals can consistently monopolise or displace subordinates from more productive (parts of) patches, allowing them to forage more efficiently (i.e. have a higher λ) than the displaced or excluded group members. Because individuals with higher foraging efficiency reach their background intake rate sooner, they are typically predicted to have an earlier optimal departure rate than individuals with a lower foraging efficiency (Davis et al. 2022). Thus, we can expect to see some links between individual traits (like dominance), optimal departure times and movement initiations.

Key to understanding the links between optimal foraging and collective departures is capturing how initiations affect future optimal departure times. Specifically, shared decision-making alters how individuals perceive the quality of their environment, which has consequences on their future decisions. From an individual's perspective, the consequence of their group leaving a patch either too late (e.g. an initiator has to wait) or too early (e.g. a follower has to prematurely abandon foraging to maintain cohesion with the departing group) is a reduction in their background rate of food intake. This change (reduction) in the background rate will then affect the optimal departure time in future patches, potentially introducing temporal contingencies across sequential decisions as a repercussion of being in a group that makes collective departures. If individuals initiate movement attempts at their predicted optimal departure times, then the MVT could explain not only why some individuals attempt to initiate movements prior to their group's ultimate departure time (because they reach this time sooner than other group members reach theirs) but also variation in who initiates across repeated departure decisions (because collective departures differentially affect the background food intake rates of group members). Thus, incorporating the process of movement initiations into the marginal value theorem is likely to yield some important insights into the dynamics of collective departure decisions. Specifically it may help explain observations that among species that form and move as cohesive groups, all, the majority of, or a consistent set of, group members make initiation movement attempts (Stueckle and Zinner 2008, King et al. 2011, Furrer et al. 2012, Gruber and Zuberbühler 2013, Strandburg-Peshkin et al. 2017, Walker et al. 2017, Sperber et al. 2019, Montanari et al. 2021, Papageorgiou et al. 2024), including both dominant and subordinate group members (Bautista et al. 1995, Lusseau and Conradt 2009, Jacobs et al. 2011b, King et al. 2011, Krueger et al. 2014, Strandburg-Peshkin et al. 2017, Wang et al. 2016, Papageorgiou and Farine 2020).

In this paper, we integrate initiation-based collective movement decisions with the marginal value theorem. There are many factors that might cause animals to form cohesive groups, including predation risk (Hamilton 1971) and same-sex competitors (Barton et al. 1996, Colmenares et al. 2006), but maintaining cohesion requires solving the collective action problem of where and for how long to forage. Despite extensive research identifying the role of movement initiations on determining both the direction and timing of group movements, we know relatively little about the dynamics of who initiates. Previous work has identified physiological state (e.g. the 'leadership according to need' hypothesis; Conradt et al. 2009, McLean et al. 2018, Papageorgiou and Farine 2020), personality (e.g. boldness, Harcourt et al. 2009, or fast explorers, Aplin et al. 2014), differences in knowledge about the presence of resources (e.g. knowledgeable individuals, Reebs 2000, or producer scrounger dynamics, Vickery et al. 1991). However, none of these provide a bottom–up answer to how movement initiations and differences in who initiates from one decision to the next can emerge.

To address the drivers and consequences of movement initiations, we incorporate waiting time into the MVT, which captures the time that an initiator spends waiting for its group members to make a collective departure decision. Waiting time comprises the period from when the individual ceases its own foraging until its group begins searching for, or moving to, a new patch. We start by demonstrating how movement initiations, and thus waiting, can reduce conflicts among group members in the timing of departures from subsequent patches. Next, we describe how combining habitat heterogeneity with MVT-based decision-making can explain the emergence of distributed leadership (where different individuals are observed initiating movements across a series of departure decisions). Finally, we use numerical simulations of collective foraging groups (using a majority rule to decide on when to depart each patch) to show that different forms of leadership and consensus decision-making can emerge under different environmental conditions.

Movement initiations can reduce conflicts in the timing of departures

When an individual reaches its predicted optimal departure time before other members of its group, it can either continue foraging until some fraction (e.g. a majority) of other group members eventually decide to leave the patch (Davis et al. 2022) or, instead, it can stop foraging and make a movement initiation attempt. Initiations likely serve to speed up collective patch departures by ensuring that there is a salient cue that (at least some) group members are ready to depart (Farine 2022, Liao et al. 2024). However, wait times experienced by an initiator decrease the background intake rate that it experiences, acting as though there is a longer travel time between patches (i.e. the total time between stopping and restarting foraging becomes $\omega + \mu$). The MVT therefore predicts that such an initiator (an individual with a high foraging efficiency, who experiences a wait time ω) will have a lower background rate $[g(t+\omega)/(\mu+t+\omega) < g(t)/(\mu+t)]$, and that this will result in a later predicted optimal departure time in future patches than it would have without any waiting time (Fig. 1A). By contrast, an individual with an optimal departure time that matches the group departure (e.g. under a majority rule, where the group leaves when more than half of the group members have initiated, this would represent the median predicted optimal departure time) will experience no future change in its predicted optimal departure time as a consequence of collective departures. Individuals with a later predicted optimal departure time than the actual time at which the group departs (i.e. an individual with a low foraging efficiency) will also have a later predicted optimal departure time than if they were foraging alone because departing the patch early also reduces their background rate. However, the effects on high and low efficiency foragers are asymmetric – making the departure time earlier will have less of an effect on the background rate of a low efficiency forager than departing late has on the background rate of a high efficiency individual (Supporting information). Thus, waiting (e.g. when initiating movement) reduces the difference between the predicted optimal departure times of the initiator and predicted optimal departure time of individuals that reach their background rate later (Fig. 1B). Initiating movement can, therefore, reduce the amount of conflict among group members by making the optimal departure times of each individual group member more similar.

Habitat heterogeneity can drive emergent leadership

When moving together and foraging as a group, individuals with higher foraging efficiency are expected to have earlier

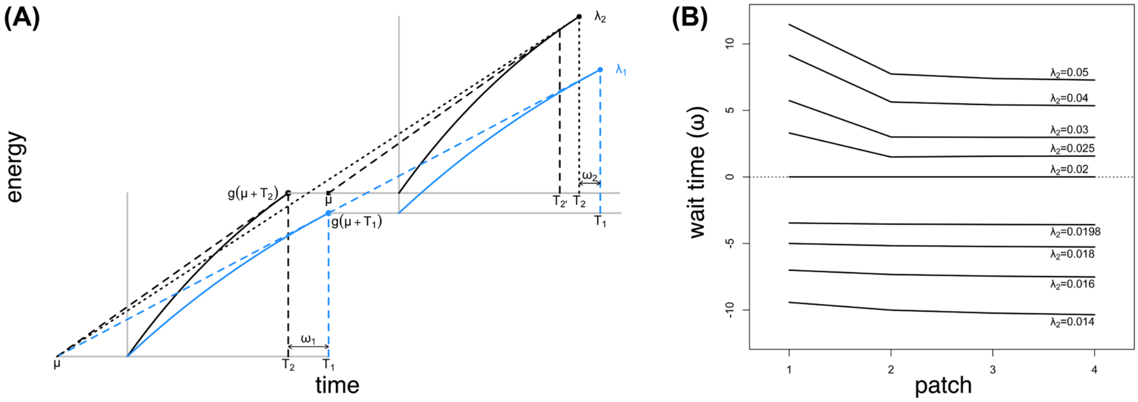

Figure 1. The effect of movement initiations (waiting) increases the predicted optimal patch departure times in subsequent patches, reduces future waiting times, and ultimately reducing conflicts of interests among members of cohesive groups where individuals have different foraging efficiencies. The marginal value theorem predicts that an individual should leave a patch when its current energy intake rate, here given by $g(t) = 1 - e^{-\lambda t}$, is equal to the background intake rate of the environment, i.e. when $g'(t) = g(t)/(\mu + t)$. Foraging efficiency (λ), which is defined as the instantaneous rate of gain when the individual enters a patch, determines how quickly individuals accumulate resources in a patch (with units of energy.time^{-1}). The λ values used (e.g. 0.02–0.05) reflect biologically plausible variation in intake rates across individuals, with higher values indicating faster foragers (e.g. dominants, adults, and/or more experienced individuals as per the literature, Livoreil and Giraldeau 1997, Eadie 2015, Hartley et al. 2019, Methion and Díaz López 2020). For example, a subordinate or less experienced individual with $\lambda = 0.02$ has a slower rate of intake, reaching ~63% of total possible gain after ~50 time units; in contrast, a dominant or more experienced individual with $\lambda = 0.05$ reaches the same level in ~20 time units. (A) A group first forages in one patch (bottom left) before moving to another patch (top right). The energy accumulation curves for two individuals, one has a higher foraging efficiency (λ_2; black, upper curve) than a median individual that represents when the group departs (λ_1; blue, lower curve). The predicted optimal departure time, given by the MVT (vertical dashed lines), for each individual is given by the tangent between its energy accumulation curve and a line starting at the point it started foraging (i.e. accounting for the travel time μ), here shown by the dashed lines. If the higher foraging efficiency individual has to wait (ω_1) for the group (represented by a lower efficiency median individual) before departing for the second patch (at T_1), then its background intake rate (dotted line) decreases proportionately to the waiting time, i.e. $g(t + \omega_1)/(\mu + t + \omega_1)$ will be smaller than $g(t)/(\mu + t)$. As $g'(t)$ is a decreasing function, and optimal foragers should respond to changes that they experience in the environment (McNamara and Houston 1985, Calcagno et al. 2020), the high efficiency individual is predicted to forage for longer at the second patch (top right, vertical dotted line) than it would have had it not waited (i.e. $T_{2'} < T_2$). As a result, the initiator's subsequent wait time is shorter ($\omega_2 < \omega_1$). Gain curves are shown with a high foraging efficiency $\lambda_2 = 0.03$ (upper line) individual and a lower foraging efficiency $\lambda_1 = 0.02$ (lower line) individual that represents the group departure, and a travel time $\mu = 10$. (B) The wait time (ω), which is defined as the difference in the optimal departure time of an individual and the departure time of the group (here $T_1 - T_2$), for a high efficiency individual decreases over consecutive patches. This generally reduces the conflict of interest in the timing of departures between the individual and other group members. The reduction in conflict is greater when the differences in foraging efficiency are greatest (here $\lambda_1 = 0.02$ for all lines). Low efficiency individuals that depart at the optimal departure time of a higher efficiency individual (Supporting information) experience a smaller change in their predicted departure time (and thus difference between their observed and predicted departure times, ω). Travel time is the same for all scenarios ($\mu = 10$), but the overall pattern is not sensitive to travel time.

preferred/optimal departure times and, thus, initiate movement. How then do initiation attempts by low foraging efficiency individuals emerge if they typically have a later predicted departure time? One key to answering this question is found in considering how the foraging dynamics in groups affect, and are affected by, the habitat heterogeneity that an individual experience. All animals experience spatio-temporal variability in patch quality in their habitat – a key question being how this variability interfaces with collective decision-making by animal groups.

The MVT predicts that solitary foragers experiencing a mixture of high quality (short μ or high λ) and low quality (long μ or low λ) patches (Fig. 2A) will experience a background foraging rate that is intermediate to both, with the precise value depending on the proportion of each patch type in the environment (Stephens and Krebs 1986, Calcagno et al. 2020). This means that when an individual is foraging in a low-quality patch, it will reach its background rate sooner if that patch is part of a heterogeneous habitat (as a consequence of the background rate being higher) than it would if the same patch was in a habitat with uniformly low-quality patches (as a consequence of the background rate being lower). Conversely, an individual foraging in a high-quality patch will reach the background rate later in a heterogeneous than in a homogeneous habitat containing only high-quality patches (because the background rate is lower in the former than in the latter). The MVT therefore predicts that in habitats with heterogeneous patch qualities, individuals will have an earlier predicted optimal patch departure time when foraging in lower quality patches and a later predicted optimal patch departure time when foraging in higher quality patches (Calcagno et al. 2014). The predicted optimal departure time for a given patch therefore depends not only on the quality of the present patch, but

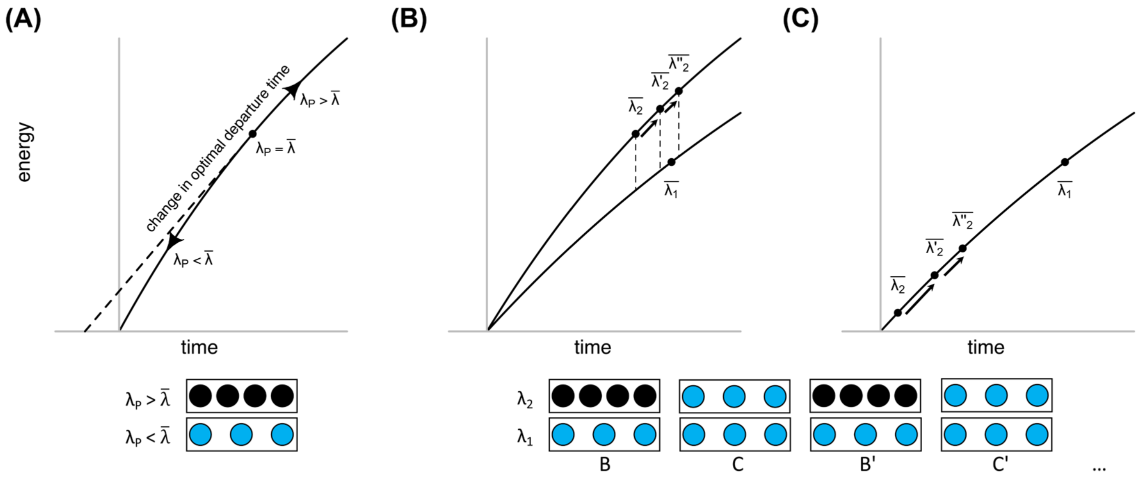

Figure 2. Variation in foraging rates across patches (between-patch heterogeneity) and differences in foraging rate among group member (within-patch heterogeneity) can affect optimal departure times, reducing differences in optimal departure times among group members and eventually causing a change in which individual has the earliest optimal departure time. (A) In heterogenous habitats, how long a forager should spend in a patch, and subsequently their optimal patch departure time, will depend on the relationship between the current patch quality (the foraging efficiency experienced when an individual begins foraging in a patch, λ_P) and the background rate (or expected foraging efficiency $\bar{\lambda}$). When encountering a high-quality environment ($\lambda_P > \bar{\lambda}$), where a forager accumulates more resources per unit time (black points), the forager is predicted to have a later optimal departure time compared to foraging in the same patch within a uniform environment (where $\lambda_P = \bar{\lambda}$). Conversely in a low-quality environment ($\lambda_P < \bar{\lambda}$), where a forager accumulates fewer resources per unit time (blue points), the forager is predicted to have a later optimal departure time. (B–C) Groups often forage in habitats containing patches where some group members can have a higher foraging rate than other group members ($\lambda_2 > \lambda_1$, e.g. B) and patches where all group members can forage equally ($\lambda_2 = \lambda_1$, e.g. C). An individual with a higher foraging efficiency (λ_2) in heterogeneous patches (B) can acquire food at a faster rate in the patch compared to a median group member (λ_1), and as a result reaches its the background rate ($\bar{\lambda}_2$) earlier than the median group member ($\bar{\lambda}_1$). When individual 2 then experiences a homogeneous patch (C), the habitat heterogeneity that it experiences will result in it reaching its background rate ($\bar{\lambda}_2$) much earlier than the median group member ($\bar{\lambda}_1$). Under collective decision-making (Davis et al. 2022), individual 2 will need to wait for a majority of group members to depart, and with learning (McNamara and Houston 1985) this wait time will decrease its background rate over consecutive patch visits (shown sequentially as $\bar{\lambda}_2$, $\bar{\lambda}'_2$ and $»_2$, alternating between patches of type B and C). The outcome of these two processes combined is a reduction in the difference between its optimal departure time and that of a median group member (Fig. 1B). Eventually, the reduced background rate from waiting can result in individual 2 having a later optimal departure time than a median group member (i.e. when it reaches $\bar{\lambda}''_2$ in B). The effect of patch heterogeneity is exacerbated by habitat heterogeneity (as individual 2 has to wait disproportionately longer when the group encounters homogenous patches). This example illustrates how movement initiations by lower efficiency individuals (like subordinates or juveniles) can occur as a function of within-group, within-patch and between-patch heterogeneity.

also on the attributes of all other patches in the environment (Calcagno et al. 2014). These effects are then expected to be further modified by waiting times and early departures for group-living animals that make initiation-based collective departure decisions.

Of particular importance for group foraging dynamics, food patches often vary in ways that impact how equally group members extract resources. For example, groups could experience a mixture of homogeneous patches, where all individuals have the same foraging efficiency, and heterogeneous patches, where some group members (e.g. dominants that can monopolise the richest parts of the patch) will experience a higher foraging efficiency than other group members (Giraldeau and Caraco 2000). Thus, a consequence of within-patch heterogeneity is that some group members can experience greater between-patch heterogeneity than other group members. Differences within groups in terms of how individuals experience within- and between-patch heterogeneity can decrease the differences in optimal departure times among group members for a given patch (Fig. 2).

The pattern discussed so far (individuals foraging longer in patches where they experience higher foraging efficiency and shorter in patches where they experience lower foraging efficiency) is exacerbated in groups where departure decisions are made collectively. Specifically, a group member that experiences greater between-patch heterogeneity (those that experience a lower foraging efficiency in some patches, e.g. individual 2 in Fig. 2) can ultimately have a lower background foraging rate. As a consequence, they will have disproportionately earlier predicted optimal patch departure times when the group is foraging in a patch where it has a lower foraging rate (i.e. switching from patches of type B–C in Fig. 2). If it makes a movement initiation at its optimal patch departure time, then over time it will experience (and learn; McNamara and Houston 1985) an even lower background rate. Eventually, this can result in it having an optimal departure time that is later than the median group member. Logically, this switch in the order of predicted optimal departure times could cause temporal variation in who initiates movements among group members.

Predicting when low foraging efficiency group members will make movement initiations

We use numerical simulations of foraging groups in which individuals initiate movement (i.e. have a wait time) when reaching their predicted optimal departure time and the group leaves the patch once a majority of group members have initiated movement. Our simulations follow the system described in Fig. 1–2, where group members vary in foraging efficiency when encountering heterogeneous patches, but have the same foraging efficiency in homogenous patches. Individuals also track changes in their background foraging rate using a simple learning rule (taking the average across previous patches visited) given by McNamara and Houston (1985). The values of λ we use (0.005–0.03) are also grounded in empirically observed foraging rates, and the variation in foraging efficiencies that group members may experience. For example, observed λ values for individuals in groups of spiced finches *Lonchura punctulata* foraging on seeds have been found to range from 0.038 to 0.063 (Livoreil and Giraldeau 1997). In wild white-faced capuchin monkeys *Cebus capucinus*, adults have been found to gain energy at approximately 0.067 units s^{-1}, while juveniles do so at 0.026 units s^{-1} (Eadie 2015). Bottlenose dolphins *Tursiops* spp. have also been found to have similar values for foraging efficiencies, ranging from 0.00 to 0.57 energy units/time depending on the individual (Methion and Díaz López 2020). Other studies have similarly found that dominance affects foraging efficiency, for instance dominant goats acquired food more than twice as fast as subordinates (Hartley et al. 2019).

We simulated groups containing $n = 31$ individuals in the main text, and provide results for groups of $n = 11$ individuals in the Supporting information. For each simulated group (visiting 100 sequential patches of varying quality), we quantify the propensity for each group member to initiate movement across sequential patch visits, and vary 1) the probability of encountering heterogeneous versus homogenous patches, 2) the extent of variation in foraging efficiency within groups when foraging at heterogeneous patches, and 3) the overall habitat quality in terms of the density of patches (lower density = longer travel time μ). The results of these simulations (Fig. 3) confirm that both high foraging efficiency individuals and individuals that experience lower efficiency in heterogeneous patches can be observed to initiate movements when the habitat is heterogeneous. Further, the relative frequency of different patch types has a large effect on which group members initiate group movement most often, whereas the extent of variation in foraging efficiency among group members when they encounter heterogeneous patches has relatively little effect on how stable or distributed leadership is among group members.

In most environments, the simulations predict that high efficiency group members should initiate more often than low efficiency individuals (Fig. 3). This is particularly the case when environmental quality is low (travel time μ is longer) and when homogenous patches rare (heterogenous patches are encountered more frequently). However, in rich (travel time μ is short) and environments where heterogenous ($\lambda_2 > \lambda_1$, Fig. 2B) and homogeneous ($\lambda_2 = \lambda_1$, Fig. 2C) patches are encountered equally often, the simulations predict that movement initiations are relatively equally distributed among group members (e.g. yellow lines in Fig. 3D–H). Across all environmental qualities, lower efficiency individuals are most likely to make movement initiations in the most heterogeneous environments (yellow lines). As habitat quality decreases (μ is longer) and in habitats that contain fewer patches where group members have differences in foraging efficiency (hence the foraging rate λ of the more efficient group members decreases), high efficiency (e.g. dominant/more experienced) individuals are predicted to initiate far more often, and the distribution of heterogeneous versus homogenous patches becomes less important in determining the emergent patterns of initiations. However, across all conditions we can expect to observe some initiations by low efficiency group members to be expressed (e.g. at least 5% of patches visited across 95% of the conditions simulated, Fig. 3).

Group size also has an impact on who is predicted to make movement initiations. In smaller groups (e.g. $n = 11$ in Supporting information versus $n = 31$ described above), we found that individuals that experience lower foraging efficiency in heterogeneous patches (e.g. subordinates) were more likely to initiate than higher foraging efficiency individuals, and across a wider set of environmental conditions. Highly efficient group members (e.g. dominant individuals) are more likely to initiate when habitat quality is low (i.e. travel time is long). Further, initiations are more equally distributed across group members for a large range of environmental conditions. Together, these results predict that a greater proportion of the group should be observed making movement initiations in smaller versus larger groups.

Finally, some animal groups may make decisions using sub-majority quorums instead of using an absolute majority. For example, rather than leaving at the predicted optimal departure time of the 16th individual in a group of 31, the group could leave after the 11th. In vulturine guineafowl *Acryllium vulturinum*, even large groups ($n > 40$) will leave, on average, when 13 individuals have initiated movement away from a foraging patch (Papageorgiou and Farine 2020). Using the same numerical simulations as above, we find that using a sub-majority impacts the distribution of leadership within animal social groups. Specifically, there is a substantial drop in the propensity for group members with intermediate foraging efficiencies at differential patches to initiate movement when groups leave after one third of the group members have initiated movement (Supporting information). These effects are also more pronounced in higher quality (shorter travel time) habitats.

Discussion

By mechanistically linking the optimal foraging strategies of individuals to initiation-based processes of collective decision-making, we demonstrate that conflicts of interest over patch departure timing can give rise to highly variable, and

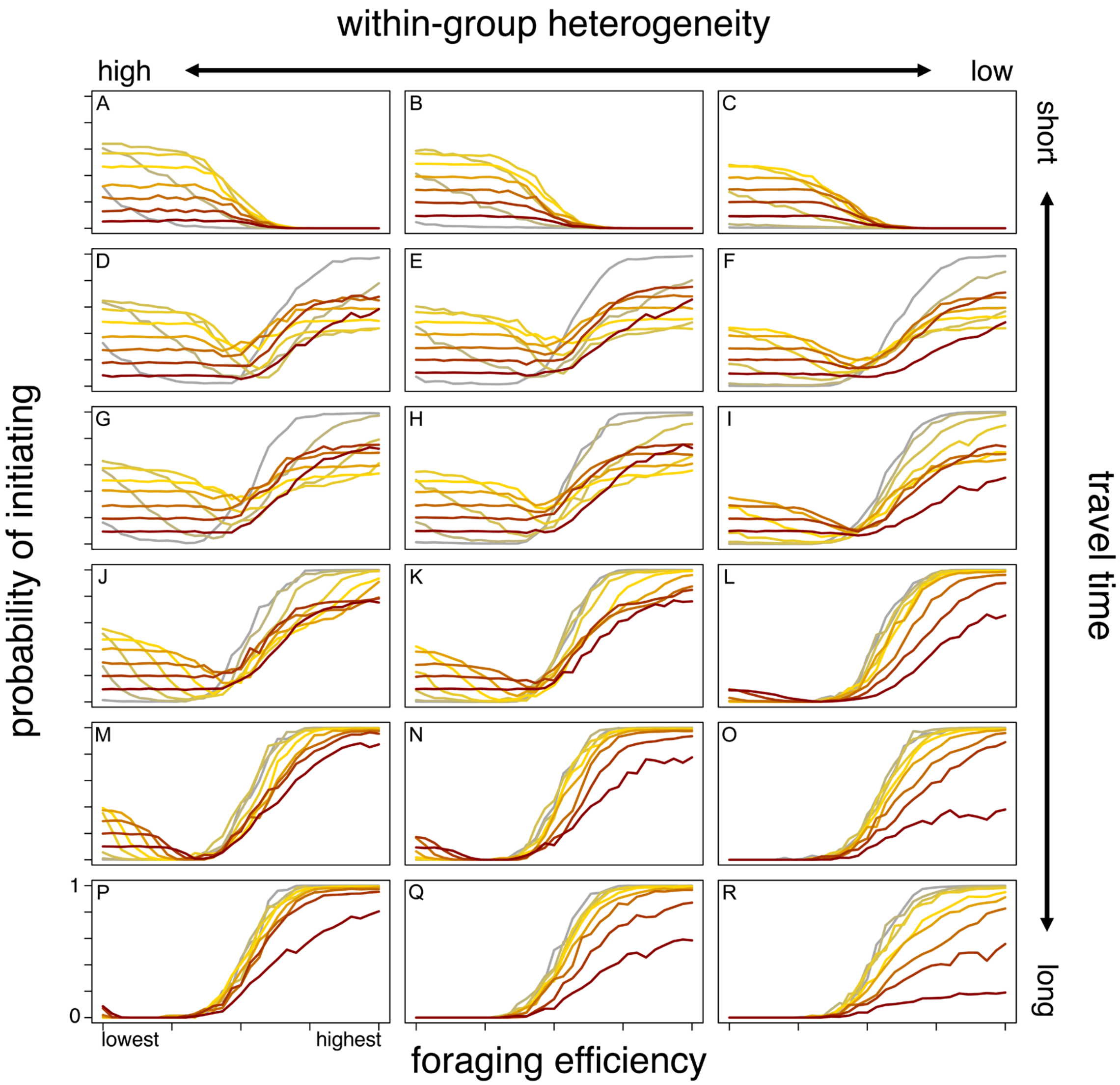

Figure 3. Variation in the extent of differences in foraging efficiency among group members in heterogeneous patches (within-group heterogeneity), the propensity for groups to encounter heterogeneous patches (between-patch heterogeneity), and environmental quality (travel time between patches) affect the probability of the highest (high λ) and lowest (low λ) efficiency group members initiating movements. Each line shows the average of 100 numerical simulations, with each simulation having a group (n = 31) forage over 100 sequential patches and making majority decisions (departing at the median, here 16th, predicted optimal departure time). Group members with a predicted optimal departure time (determined by their individually learnt background rates) that was earlier than the median predicted optimal departure time initiated movement and waited until the group departure. At homogeneous patches (all group members can forage equally, per Fig. 2C), group members the given same foraging rate (λ = 0.03). At heterogenous patches, we reversed the patch differences shown in Fig. 2, such that high foraging efficiency individuals had a maximum of λ = 0.03 (e.g. dominants) and low foraging efficiency group members had a minimum ranging from λ = 0.005 (high within-group heterogeneity) to λ = 0.02 (low within-group heterogeneity). In each simulation, foraging efficiency (λ, x-axis) values for each group member in the heterogeneous patches were drawn at random from a uniform distribution, and kept constant for the whole simulation. Thus, the individuals experiencing a constant decrease in efficiency when foraging on heterogeneous patches ranged from 1/6th to 1/3rd the most efficient group members. Travel times ranged from μ = 0.2 (shortest, highest environmental quality) to μ = 5 (longest, lowest environmental quality). Line colours represent the probability that the group would encounter a heterogeneous patch (grey = 0.1, yellow = 0.5, dark red = 0.9, in steps of 0.1), capturing different habitat compositions and extent of between-patch heterogeneity (yellow lines are the most heterogeneous environments). For each patch, we recorded the identity of the group members that contributed to a movement initiation (i.e. had a wait time ω > 0).

sometimes counterintuitive, patterns of leadership in cohesively foraging animal groups – as is often observed in nature (Stueckle and Zinner 2008, Harcourt et al. 2009, Petit and Bon 2010, Jacobs et al. 2011a, King et al. 2011, Furrer et al. 2012, Gruber and Zuberbühler 2013, Pyritz et al. 2013, Ramos et al. 2015, Strandburg-Peshkin et al. 2017, Walker et al. 2017, Sperber et al. 2019, Wang et al. 2020, Montanari et al. 2021, Papageorgiou et al. 2024). First, while waiting for consensus to build can introduce costs for initiators (their foraging rate decreases), these waiting costs can act to reduce the conflict across group members over the timing of future patch departures by reducing the differences in the predicted optimal departure times across group members. Second, even when some individuals are predicted to consistently have earlier patch departure times (e.g. dominant or more experienced individuals with higher foraging efficiency), we can still observe a mix of initiators (including initiations by subordinate and/or inexperienced group members) when groups forage in heterogeneous environments. The distribution of initiators – how often high versus low efficiency group members make initiations – is determined by a multitude of factors, including the extent of variation in foraging efficiency within the group, the distribution of different patch types, the relative abundance of different patch types in the habitat, group size, and how decisions are made by the group (e.g. a full majority versus a sub-majority). Finally, across almost all parameter space we observe that initiations are at least in some part distributed among group members.

Shared decision-making is quite widespread across animal groups, and decisions in groups with stable membership are often instigated by initiation movement attempts (cf. Miller 1921 for an early description). However, to date there has been relatively little theory to explain how and why initiations of this type exist. Given that social animals face tight time budgets, and clear tradeoff exists between maintenance and discretionary activities (e.g. food supplementation increases social behaviour; Garcia et al. 2021), it seems counterintuitive for individuals to stop (or mostly stop) foraging to initiate movement. These initiations are also distinct from other self-maintenance behaviours, as they typically involve a directed movement away from the foraging patch (reviewed by Liao et al. 2024). By contrast, scanning for predators is typically interspersed with foraging (Scannell et al. 2001), and thus reduces foraging rate g(t) (Fernández-Juricic et al. 2004), but generally does not involve moving away from the patch (an exception are sentinels). As we have shown here, the dynamics of who initiates and when may not be driven by the social environment alone (i.e. who is dominant or who can exert influence on the group). Instead, the timing of individuals' decisions to stop foraging and move away from a food patch could also be driven by the interaction between within-group dynamics (e.g. variation in foraging rates among individuals) and environmental conditions (including the history of what types of patches the group has visited and how long it has taken them to travel between them).

In general, we found that the reduction in waiting times for efficient foragers gets flatter over time (Fig. 1B). This is a result of the background rates becoming more similar among group members. Initiators have a higher foraging rate than followers, and waiting decreases this foraging rate. We also found that changes in waiting time for initiators from one patch to the next is larger than the increase in waiting time caused by having to leave a patch early. This asymmetry is key to reducing the range of wait times among group members (e.g. the range of y values in Fig. 1B over multiple patches), and ultimately reducing conflict in terms of differences in their optimal patch departure times. One outstanding question is how this emergent phenomenon plays out across the different conditions experienced by animal groups (i.e. different λ_i, ω_i and μ values). Future work exploring the properties of the marginal value theorem for cohesive groups, e.g. using analytical approaches, may find some important properties that will have significance for our empirical understanding of how animal groups make collective departure decision (Kao et al. 2024).

We found that how equally all individuals initiate movements depends on a diverse set of factors. These include both environmental factors, such as how densely packed patches are in the environment (i.e. how long the travel time is) and the proportion of the patches where group members experience differences in foraging rates. What is particularly interesting, and which has been noted by many authors before (including Giraldeau and Caraco 2000, Calcagno et al. 2014, Davis et al. 2022), is that universal changes in the abundance of food within a patch do not alter the timing of predicted optimal departure times. This means that the dynamics reported here are largely invariant to what proportion of the available food each individual gains. Rather, as we have demonstrated, the relative rate at which group members can extract their 'share' of the patch has major consequences on the distribution of optimal departure times. There are many scenarios in which differences in foraging efficiency among group members can arise. Examples that we have mentioned include differences in skill, which maybe be more important at some food sources than others. In some cases, such as when social dominance dictates who can access parts of patches with higher foraging efficiency, differences can arise even when all group members would otherwise have exactly the same foraging efficiency if they experienced the patch as solitary foragers. In other words, social dynamics alone can produce divergences in optimal departure times among individuals that would otherwise have the same optimal departure time if they foraged independently.

Within a group, we found that how decisions are made can have an impact on the distribution of initiators that are expected to contribute to group decisions across repeated departures. Specifically, groups that departed after a lower number of initiators (a so-called sub-majority, Conradt and Roper 2005) had fewer initiations by individuals with intermediate foraging efficiencies. Sub-majority decisions are often expressed in contexts with temporal urgency – capturing a speed versus accuracy tradeoff in decision-making (Chittka et al. 2009, Liao et al. 2024). For example, group initiations when a predator is spotted may require a threshold of only two or more individual initiators (Lima 1995) because the fitness cost of not responding when a predator attacks is high. The marginal value theorem should promote departing when a sub-majority of the group have initiated because the opportunity cost of leaving early (when the foraging rate is higher) is greater than the opportunity cost of leaving late by the same amount [i.e. the difference between $g(t)/(\mu + t)$ and $g(t+\omega)/(\mu + t + \omega)$ for a fast forager is smaller than the difference between $g(t)/(\mu + t)$ and $g(t-\omega)/(\mu + t - \omega)$ for a slow forager, as $g(t)$ has a decreasing rate]. Thus, departing when there are few initiators (i.e. on average earlier) would result in an overall smaller decrease in the background foraging rates across all individual group members because it causes groups to leave patches earlier. However, if it is important to have more decision-makers involved (e.g. to benefit from the collective benefits, Ogino and Farine 2024), then individuals with early optimal departure times may choose to remain longer in the patch. In nature, it has been observed that many organisms preferentially remain longer than expected in foraging patches rather than leaving early (Nonacs 2001). One interesting recent prediction (Davis et al. 2022) is that the optimal decision threshold could be the point where the number of group members initiating most closely matches the predicted optimal departure time from the group's gain curve, as this will maximise the average background intake rate across all group members (i.e. the total amount of resources that the group as a whole extracts from the environment). Future studies may explore at what proportion of the group have an optimal departure time that closely matches the group-level optimal departure time, and how this is affected by various environmental and social factors. Evolutionary game theoretic models may also be able to test this prediction explicitly by allowing the threshold at which a quorum is reached to evolve, and determining whether this converges on the group-level optimal departure time.

One nice feature of the marginal value theorem is that it can quite easily be tested under field conditions (even when food 'patches' are not discernible, Pacheco-Cobos et al. 2019). The predictions from this paper, for example, can be tested by observing foraging individuals as they make repeated initiations over time. We predict that if initiations are in part driven by individuals responding to their predicted optimal departure times, then we should find that individuals initiate as their intake rate reaches approximately the same value across different patches (i.e. their background rate). Such observations need not come from sequential patches, but rather could be made from repeated quantification (even in non-consecutive patches) of the rate at which individuals stop foraging and start making an initiation movement. Other factors, for example displacements (Papageorgiou and Farine 2020) or satiation (Marshall et al. 2013), could cause individuals to initiate at higher rates or to stop foraging but not initiate, respectively. However, with close behavioural observations (e.g. the foraging behaviour of individuals in subsequent patches, and whether they previously initiated or not) and observations made when group members are highly food motivated (e.g. early in the morning) should yield sufficient data to test that the MVT can predict movement initiations.

A final point of note is the question of how animals deal with the dynamic nature of the environment that they experience. If optimal foraging drives initiations, as suggested here, this demonstrates an excellent example of an individual–environment social feedback loop (Cantor et al. 2021). In this case, the social environment modifies how individuals experience their environment (here, the background foraging rate), which affects social interactions (the timing of movement initiations), and, in turn, further modifies how individuals experience their environment (by updating their background foraging rate). Such dynamics could be further affected by changes in predation pressure or changes in social structure that cause individuals to alter the amount of time they spend scanning outside and/or inside the group, respectively (Fernández-Juricic et al. 2004); and thus the rate of energy gain $g(t)$. The consequence of this, however, is that the background foraging rate is unlikely to remain fixed in time. Most models that use the MVT make the original assumption stated by Charnov (1976) that animals have knowledge of the long-term rate of the environment. However, this is not strictly necessary, as models have also demonstrated that individual animals can estimate, and closely approximate, the true background rate and that learning can be modified by increasing weighting on recent experience to track changing environments (McNamara and Houston 1985). We did not explore the consequences of different updating strategies, as our baseline environment remained fixed and thus individuals should converge on a true rate for each individual. However, group membership – or the roles individuals play within their group – can also change rapidly (Strauss 2023), and individuals may benefit from rapid updating following such changes. Finally, groups are likely to benefit from using different departure rules under different conditions – for example employing a more rapid threshold (fewer initiators) for departures in response to predator attacks (Lima 1995) than departures caused by patch depletion or requiring a super-majority to move away from more beneficial habitats (Strandburg-Peshkin et al. 2017). Our results could thus be further extended by testing whether different (or changes in) environmental conditions could drive dynamic majority thresholds to maximise the benefits to efficient and inefficient foragers. Such questions highlight the value of exploring the MVT for understanding the dynamics of movement and decision-making by animal groups.

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Author contributions

Damien R. Farine: Conceptualization (lead); Formal analysis (lead); Investigation (lead); Methodology (lead); Writing – original draft (lead); Writing – review and editing (lead). **Grace H. Davis**: Conceptualization (supporting); Formal analysis, Methodology, Writing – original draft, Writing – review and editing. **Margaret C. Crofoot**: Conceptualization, Methodology, Writing – original draft, Writing – review and editing.

Data availability statement

Data are available from Figshare: https://figshare.com/s/bad3e949ef326563ff13 (Farine et al. 2025).

Supporting information

The Supporting information associated with this article is available with the online version.

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