Received: 25 October 2021 | Revised: 8 December 2021 | Accepted: 9 February 2022

DOI: 10.1111/ele.13988

ECOLOGY LETTERS cnrs WILEY

PERSPECTIVE

The important role of animal social status in vertebrate seed dispersal

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Editor: Robin Snyder

Abstract

Seed dispersal directly affects plant establishment, gene flow and fitness. Understanding patterns in seed dispersal is, therefore, fundamental to understanding plant ecology and evolution, as well as addressing challenges of extinction and global change. Our ability to understand dispersal is limited because seeds may be dispersed by multiple agents, and the effectiveness of these agents can be highly variable both among and within species. We provide a novel framework that links seed dispersal to animal social status, a key component of behaviour. Because social status affects individual resource access and movement, it provides a critical link to two factors that determine seed dispersal: the quantity of seeds dispersed and the spatial patterns of dispersal. Social status may have unappreciated effects on post-dispersal seed survival and recruitment when social status affects individual habitat use. Hence, environmental changes, such as selective harvesting and urbanisation, that affect animal social structure may have unappreciated consequences for seed dispersal. This framework highlights these exciting new hypotheses linking environmental change, social structure and seed dispersal. By outlining experimental approaches to test these hypotheses, we hope to facilitate studies across a wide diversity of plant-animal networks, which may uncover emerging hotspots or significant declines in seed dispersal.

KEYWORDS
dominance hierarchy, endozoochory, frugivory, global change, movement ecology, omnivory, plant-animal interactions, seed dispersal, social behavior, social structure

INTRODUCTION

Seed dispersal is a fundamental process for the survival, reproduction and spread of plants because it is the only stage in the plant life cycle when many plants may use movement to colonise new habitats, escape competition or evade attack by pathogens and herbivores (Carlo & Tewksbury, 2014; Hirsch et al., 2012; Howe & Miriti, 2000, 2004; Howe & Smallwood, 1982; Jordano, 2000; Schupp et al., 2010). Animal-mediated seed dispersal is among the most common modes of seed dispersal (Herrera & Pellmyr, 2002; Howe & Smallwood, 1982; Jordano, 2000); 64% of gymnosperm and 27% of angiosperm plant species rely on vertebrates for dispersal (Herrera, 1989b). As a result, understanding patterns in animal-mediated seed dispersal (zoochory) may provide a means to predict spatial patterns in plant recruitment (Beckman & Rogers, 2013), how plant species may respond to climate change (Cain et al., 2000; Corlett & Westcott, 2013; Dyer, 1995; González-Varo et al., 2017, 2021; Kremer et al., 2012; Naoe et al., 2016, 2019) and the outcomes of exotic plant invasions (Baltzinger et al., 2019; Traveset & Richardson, 2014). However, zoochory is notoriously variable in both the quantity of seeds dispersed and distance of seed movement (Côrtes & Uriarte, 2013; Rogers et al., 2019; Schupp et al., 2010). Consequently, developing predictive

frameworks that enable more effective classification and prediction of zoochory has been an ongoing challenge to ecologists for several decades (Côrtes & Uriarte, 2013; Donoso et al., 2020; Rehm et al., 2019; Rogers et al., 2019; Schupp et al., 2010; Sorensen et al., 2020; Zwolak, 2018; Zwolak & Sih, 2020).

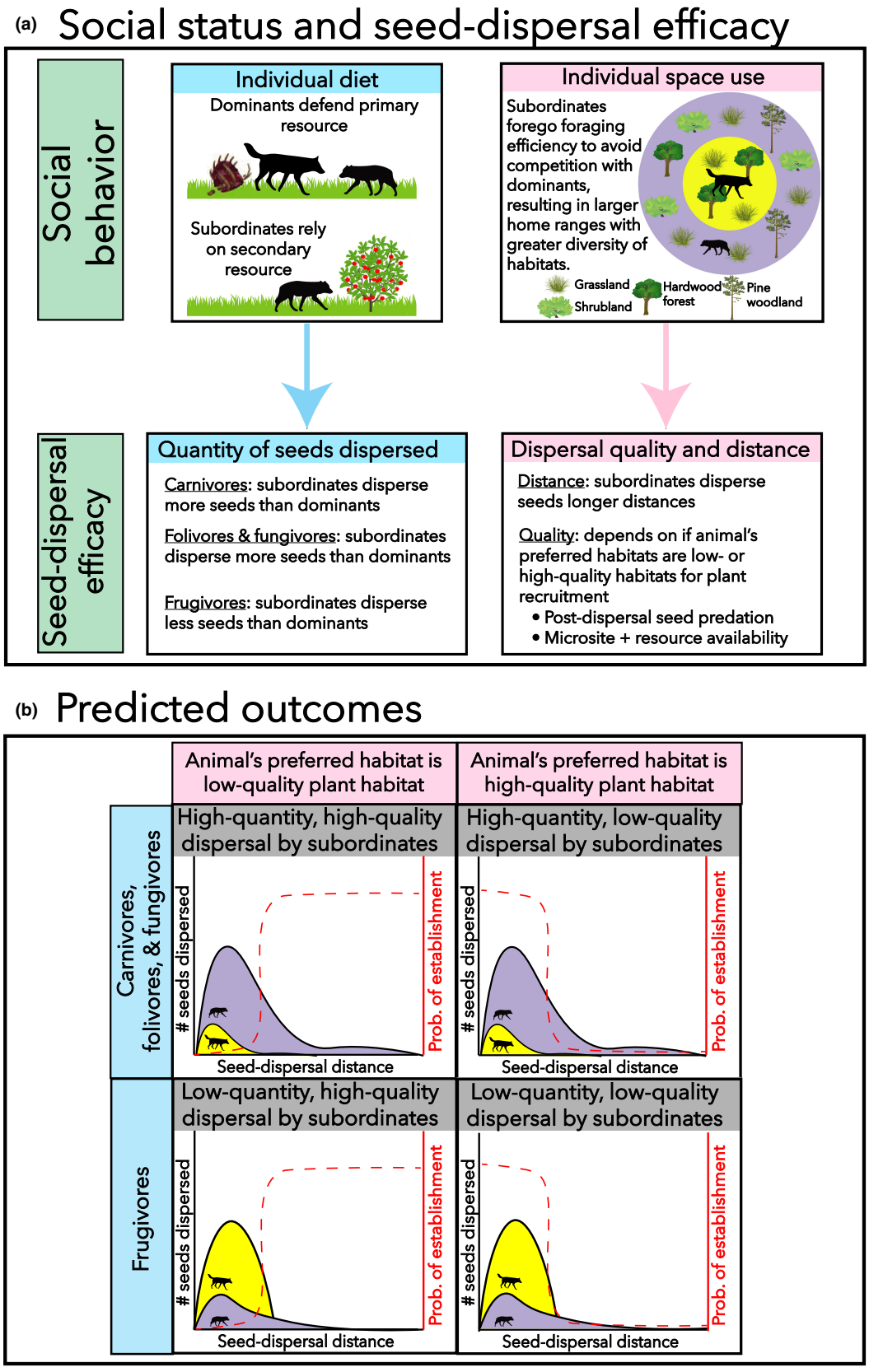
Although studies have shown that animal behaviour provides a useful means for predicting spatial patterns in plant recruitment (Beckman & Rogers, 2013; Herrmann et al., 2016; Kremer et al., 2012; Levey et al., 2005; Russo et al., 2006; Sasal & Morales, 2013; Wang & Smith, 2002), high intraspecific variability in the behaviour of seed-dispersal agents can limit our ability to understand patterns in seed dispersal (Zwolak, 2018). High intraspecific variation in disperser efficacy may have important pragmatic ramifications because species-level averages of disperser efficacy (i.e., mean number of seeds dispersed by individuals of one species) are often used to predict how changes in animal populations and communities may lead to losses in seed dispersal (e.g. Culot et al., 2017; Peres et al., 2016). For example, realised seed dispersal in fragmented habitats will be much lower than what is predicted by a species-average approach if individual animals that provide disproportionately greater contributions to seed dispersal are also the individuals most likely to be lost or exhibit changes in behaviour in fragmented habitats (McConkey & O'Farrill, 2016; Zwolak, 2018). As such, identifying traits of dispersal agents that explain intraspecific variation in behaviour may provide the key to successfully predicting seed dispersal (Brehm et al., 2019; Côrtes & Uriarte, 2013; González-Varo et al., 2019; González-Varo & Traveset, 2016; Schupp et al., 2017; Zwolak, 2018; Zwolak & Sih, 2020). Specifically, identifying individual traits that may affect the quantity of seeds handled, the distance that seeds are carried, and the microhabitat in which seeds are dispersed is critical to predicting variation in the effectiveness of individual agents of seed dispersal (Brehm et al., 2019; Schupp et al., 2010).

Social status, which may reflect an individual's age, size, sex or rank in a dominance hierarchy, may have an important bearing on individual behaviours that directly and indirectly affect seed dispersal by animals. The effectiveness of seed-dispersal agents is described as the 'number of new adults produced by the dispersal activities of a disperser' (Schupp, 1993). Seed-dispersal effectiveness is the product of the quantity of seeds dispersed (quantity component) and the probability of seedling establishment (quality component; Schupp et al., 2010). Because social status can affect individual diet composition, social status may help predict intraspecific variation in the quantity of seeds dispersed (Figure 1). Recent work by Tsuji et al. (2020) provides compelling evidence that social rank in Japanese macaques determines the quantity of seeds dispersed by an individual, and we suggest that this may be applicable for a broad diversity of taxa, ranging from species with solitary dispersed social systems to those that form large groups with dominance hierarchies (Table S1). We also highlight that social status affects individual space use, which may help explain intraspecific variation in both the distance and quality of seed dispersal (Figure 1). Some of the unresolved variation in seed dispersal could, therefore, be understood by a novel focus on animal social status.

We present a framework that provides important clarity on the relationships between individual social status, animal behaviour and seed dispersal, allowing for predictions of seed-dispersal patterns across a variety of systems. This framework may also be used to understand how animal social behaviour affects our ability to mitigate several timely ecological challenges, such as biological invasions, plant persistence in urban environments, and plant persistence amidst climate change. We highlight that in many systems, subordinate individuals may be key agents of seed dispersal, illustrating that individuals with minimal demographic contributions may have substantial ecological contributions, that is, subordinate animals may play a dominant role in seed dispersal. Hence, environmental changes that affect animal social structure may have unappreciated consequences for seed dispersal. This framework is informed by two perspectives of how social status may affect the quantity of seeds dispersed as well as the quality and distance of dispersal. This framework will be useful in systems where plant species are dispersal limited, animal social status affects individual resource access and movement, and fruit is a component of the focal animal species' diet. Although our framework specifically focuses on endozoochory, the general concepts and hypotheses that we present could be applied to other forms of animal-mediated dispersal (e.g. dispersal of ectozoochorous seeds that adhere to the outside of an animal or dispersal of fungi or parasites) that are mediated by individual diet and space use.

SOCIAL STATUS AFFECTS THE QUANTITY OF SEEDS DISPERSED

Social status is often predictably related to an individual's ability to defend preferred food items (Ward & Webster, 2016a), which likely generates intraspecific variation among dispersal agents in the quantity of seeds they disperse. This variation in seed dispersal may be most evident in two general types of systems: 1) where fruit is a supplementary food item that is less preferred to a food item that can be defended by dominant individuals, leading to greater quantities of seeds dispersed by subordinate individuals supplementing their diets with fruit and 2) where fruit is the preferred food item that is defended by dominant individuals, leading to greater quantities of seeds dispersed by dominant individuals than subordinates (Figure 1). For example, coyotes (*Canis latrans*) are social carnivores with highly variable diets that often



include fruit (Mastro, 2011; Parker, 1995), and fruit consumption by coyotes can provide seed-dispersal services for a wide range of plant species across North America (Bartel & Orrock, 2021; Cypher & Cypher, 1999; Draper et al., 2021; Roehm & Moran, 2013; Willson, 1993). Because coyote dominance hierarchies affect individual access to carrion (i.e., dominant individuals have greater access than subordinates; Atwood & Gese, 2008; Gese

FIGURE 1 (a) Social status has predictable effects on individual resource access and space use that may explain individual-level variation in seed-dispersal effectiveness. Dominant individuals defend preferred resources, forcing subordinate individuals to supplement their diets to a greater extent with secondary resources. Subordinate individuals may then disperse disproportionately more or less seeds than dominant individuals, depending on whether fruit is the primary or secondary resource. While this hypothesis has been supported in recent work on Japanese macaques (Tsuji et al., 2020), our framework demonstrates that this hypothesis could be applied to a broad range of taxa. Our framework is also novel in its demonstration of how social status may affect spatial patterns of seed dispersal, with clear consequences for seedling establishment. Dominant individuals (yellow shading) typically defend territories with preferred habitat types, and subordinate individuals (purple shading) generally have less restricted home ranges, sample more habitat patches during a foray, and are more likely to go on extraterritorial forays. Subordinate individuals are consequently more likely to move seeds greater distances and deposit seeds in a broader diversity of habitat types. Because post-dispersal seed survival and plant recruitment are likely to vary across different habitats in a landscape (e.g. differences in granivore abundance or resource availability), the quality of seed-dispersal services provided by subordinate individuals may differ substantially from dominant individuals. (b) We provide predictions for the different types of seed-dispersal kernels that may arise due to animal social behaviour, highlighting that the outcome depends on food and habitat preferences of the animal dispersal agent

et al., 1996), it is likely that subordinate individuals consume greater amounts of fruit (a secondary food item), transporting substantially greater quantities of seeds than dominant individuals (Figure 1). Because transient (less-dominant) coyotes also have reduced access to ungulate carcasses than territorial (more-dominant) individuals (Gese, 2001), it is likely that resident status is an important predictor of individual fruit consumption, and subsequent seed dispersal, in coyote populations. It may be quite common that subordinate individuals disperse substantially more seeds than dominant individuals within carnivore populations (Box 1) as well as many primate populations where social status is known to dictate individual diet breadth. For example, in Kenya, fungivorous vervets (*Cercopithecus aethiops*) exhibit rank-dependent diet breadth. High-ranking female vervets females are able to defend fungi, a larger component of high-ranking female diets, due to its abundance in restricted areas (Isbell et al., 1999). As a result, lower-ranking females incorporate significantly more fruit in their diets (Isbell et al., 1999) and are, therefore, likely to disperse greater quantities of seeds than high-ranking females.

Rank differences in seed-dispersal efficacy may also be the opposite in animal populations where fruit is both preferred and defended by high-ranking individuals. For example, American robin (*Turdus migratorius*) populations often contain territorial individuals (typically adults) that defend fruit-bearing trees as well as non-territorial individuals (typically juveniles) who intrude on territories to steal fruit (Sallabanks, 1993; Vanderhoff & Eason, 2008). Because territorial robins consume more fruits per feeding bout than non-territorial, intruder robins (Sallabanks, 1993; Vanderhoff & Eason, 2008), it is likely that territorial individuals disperse disproportionately greater quantities of seeds than intruders. We anticipate that this difference in the quantity of seed-dispersal services between territorial and non-territorial individuals could be found in a number of avian populations where fruit-bearing trees may be defended against non-territorial individuals (e.g., *Turdus viscivorus* and *Turdus pilaris*; Skórka & Wójcik, 2005; Skórka et al., 2006). Dominant individuals are also expected to disperse greater quantities of seeds in primate populations where fruit is the preferred resource. For example, in both blue monkeys (*Cercopithecus mitis stuhlmanni*) and chimpanzees (*Pan troglodytes*), high-ranking individuals consume significantly more fruit than low-ranking individuals, which consume significantly more foliage (Murray et al., 2006; Pazol & Cords, 2005). Predicting how dominant and subordinate individuals vary in effectiveness as seed-dispersal agents, therefore, requires an understanding of which food item (fruit or an alternative resource) is both preferred and able to be defended by dominant individuals (Figure 1).

Although published examples of this perspective come from mammals and birds, we anticipate that this perspective might be applied to reptile and fish species in which fruit is a component of the diet, fruit consumption facilitates seed dispersal and social status affects resource access. However, more data on these taxonomic groups is needed to determine whether our framework could be applied in these systems. Although some species of frugivorous reptiles and fish are known to disperse seeds (Anderson et al., 2009, 2011; Corlett, 2017; Costa-Pereira & Galetti, 2015; Hanish et al., 2020; Piazzon et al., 2012; Platt et al., 2013; Valido & Nogales, 1994), the effects of these taxa on seed-dispersal patterns are notably understudied (Costa-Pereira & Galetti, 2015; Genes & Dirzo, 2022). Moreover, reptilian social systems can be highly diverse and complex, yet disproportionately understudied compared with other vertebrate taxa (Doody et al., 2013). Research that investigates how social behaviour affects seed dispersal by reptiles and fish could provide new insights into the role of social interactions in mediating seed-dispersal patterns in these systems. For example, some species of solitary lizards exhibit social attraction to fruit resources (e.g., *Podarcis lilfordi* and *Ameiva corax*; Eifler & Eifler, 2014; Pérez-Cembranos & Pérez-Mellado, 2015) in which the presence of conspecifics at a resource may be a cue of patch richness (Pérez-Cembranos & Pérez-Mellado, 2015). Because aggressive behaviour among foraging lizards at fruit resources has been documented when the resources are moderately limited (Eifler & Eifler, 2014) and larger individuals are more capable of moving and opening fruit (Eifler et al., 2016), it is possible that larger, more

Box 1 Carnivores as variable seed-dispersal agents

Carnivores can be important agents of directed, long-distance dispersal (González-Varo et al., 2013; Hämäläinen et al., 2017; Herrera, 1989a; Hickey et al., 1999; Jordano et al., 2007; Koike et al., 2011; López-Bao et al., 2015; Rost et al., 2012; Shakeri et al., 2018; Tsuji et al., 2016; Willson, 1993), and rodent aversion to carnivore scat promotes the survival of scat-dispersed seeds (Bartel & Orrock, 2021). Individual niche specialisation (i.e., where intraspecific variation in seed-dispersal effectiveness should be most pervasive) is most common in upper trophic levels (Araújo et al., 2011), and many carnivore species exhibit high intraspecific variability in diet composition (Cypher et al., 2014; Darimont et al., 2009; Davis et al., 2015; Dumond et al., 2001; López-Bao & González-Varo, 2011; Manlick et al., 2019; Newsome et al., 2015). For carnivore populations with dominance hierarchies, rank can constrain individual resource access (Gese et al., 1996; Tilson & Hamilton, 1984; Zimen, 1976, 1981) and space use (Dorning & Harris, 2017; Gese, 2001; Henry et al., 2005; Kamler et al., 2019), which likely produces predictable intraspecific variation in the quantity and distance of seeds dispersed. Below, we describe two carnivore species where recent work on social behaviour indicates that social structure may predict individual seed-dispersal effectiveness.

BLACK-BACKED JACKAL (*CANIS MESOMELAS*)

Black-backed jackals have the potential to be effective seed-dispersal agents when fleshy fruit, a supplementary resource, is included in individual diets (Do et al., 2009; Kamler et al., 2020). Although it has not yet been evaluated whether individual rank within the dominance hierarchy affects fleshy fruit consumption in this species, it has been shown that rank affects individual space use such that subordinate individuals move farther distances and are more likely to go on extraterritorial forays (Kamler et al., 2019), likely increasing the distance that seeds are moved and the diversity of habitats where seeds arrive.

BROWN BEAR (*URSUS ARCTOS*)

Brown bears consume the fleshy fruit of at least 101 plant species spanning 24 families and 42 genera (García-Rodríguez et al., 2021). A single faecal deposit from a brown bear can contain thousands of seeds (Willson, 1993), creating a massive seed-dispersal event. While brown bears do not form cooperative packs, social dominance and subordination within populations has predictable effects on individual resource access and space use. In salmon-supported populations, dominant individuals (typically large males) displace subordinate individuals (particularly females with cubs) at salmon streams (Ben-David et al., 2004; Gende & Quinn, 2004). Because time spent at a salmon stream is positively correlated with salmon assimilation in brown bear diets and negatively correlated with plant matter assimilation (Deacy et al., 2018), it is likely that the defense of salmon streams by dominant individuals leads to consistently greater quantities of seed-dispersal services by subordinate individuals. Moreover, because the vast majority of long-distance movement by bears is done by dispersing subadults (Bartoń et al., 2019), these subordinate individuals are most likely to disperse plant species beyond current range boundaries (Figure 3a). Lamb and colleagues (2020) also show that urban habitats serve as demographic sinks for brown bear populations, and urban populations are supported by immigration by dispersing subadults. These subordinate, subadult bears may, therefore, contribute substantially to the dispersal and persistence of some plant populations in urban areas (Figure 3b). Because hunters typically target resident male bears (Gosselin et al., 2017; Leclerc et al., 2019), this form of selective harvest disrupts brown bear social structure, leading to increased infanticide when immigrant males disperse into newly opened territories (Gosselin et al., 2017). Whether or not the persistent disruption of brown bear social structure by selective harvesting generates cascading effects on seed dispersal remains an open question. Moreover, it is widely appreciated that brown bears use corridors to access otherwise isolated habitat patches, and corridors are particularly important for the dispersal of subadults into urban habitats (Clevenger & Waltho, 2005; Ford et al., 2017; Lamb et al., 2020). Corridors designed to facilitate brown bear movement through fragmented landscapes may, therefore, have unappreciated benefits for the dispersal of many bear-dispersed plant species.

dominant individuals may have greater access to fruit resources and consequently disperse a greater quantity of seeds. As this example demonstrates, although the components necessary for socially mediated seed dispersal are present in this system, future studies are needed to determine the degree to which it occurs.

THE DISTANCE AND QUALITY OF SEED DISPERSAL MAY VARY WITH SOCIAL STATUS

Social status predictably impacts individual space use such that social status may be used to predict the distance and quality of seed dispersal, specifically characteristics of deposition sites that affect the probability of post-dispersal predation and seedling establishment (e.g., suitable microsite availability and abundance of natural enemies: Schupp, 1993; Schupp et al., 2010). In systems where a resource can be defended (e.g., fruiting trees), the defense of resources by dominant, territorial individuals can create situations where subordinate intruders steal defended resources and then move far away to avoid antagonistic encounters, thereby elongating seed-dispersal kernels (Box 2, Figure 2a). The contrast in space use between territorial, dominant individuals and intruding subordinates has been explicitly linked to patterns in seed dispersal in a study of flying foxes (McConkey & Drake, 2006). However, intruding behaviours by subordinates have been documented in a variety of taxa, including birds, primates, and bats (McConkey & Drake, 2006; Sallabanks, 1993; Skórka et al., 2006; Skórka & Wójcik, 2005; Tsuji et al., 2020; Vanderhoff & Eason, 2008; Ward & Webster, 2016b), indicating that this is a potentially profitable, yet largely untapped area of research that may elucidate patterns in seed-dispersal kernels.

For large, group-living mammals, an individual's rank within a dominance hierarchy has well-documented effects on its movement across landscapes. Dominant individuals often have more restricted home ranges, spending more time in predictable, preferred habitat types (Aycrigg & Porter, 1997; Dorning & Harris, 2017; Henry et al., 2005; Kamler et al., 2019; Wittemyer et al., 2007). Subordinate individuals often forego foraging efficiency to mitigate competition with dominants (Dorning & Harris, 2017; Gilbert-Norton et al., 2013; Henry et al., 2005), and this increased movement likely leads to an increase in the diversity of habitats in which seeds may be deposited as well as increased dispersal distance (Figure 1). Broader distinctions between territorial and transient individuals may also be used to predict spatial patterns in seed dispersal and recruitment. For example, territorial males in lekking blackbuck antelope (*Antilope cervicapra*) populations defecate in dung piles, leading to spatially concentrated patterns of seed arrival within male territories and substantially higher rates of seedling recruitment on territories than on random sites (Jadeja et al., 2013). Because non-territorial males in mixed-sex herds range over large areas and do not predictably deposit seeds in dung piles (i.e. high-quality sites for plant recruitment; Jadeja et al., 2013), seed dispersal by non-territorial individuals is likely lower in quality due to the quality of the deposition site for plant recruitment. This example highlights that commonly used methods for estimating seed dispersal that rely upon individual movement patterns and gut-retention time may not accurately capture intraspecific variation in dispersal efficacy if the quality of deposition site for plant recruitment is not also evaluated. Important factors determining the quality of the deposition site that may affect the probability of plant recruitment and are likely to vary across habitats include competitor density, probability of attack by granivores and other natural enemies, and resource availability (Rogers et al., 2019; Schupp et al., 2010, 2017).

Because individual movement and habitat use is affected by social status, the quality of seed-deposition sites may vary among individuals of different social statuses

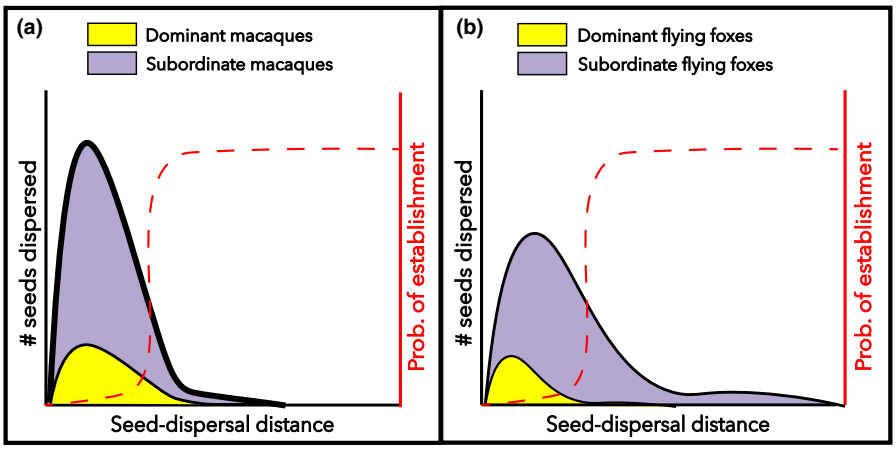


FIGURE 2 We provide predicted seed-dispersal kernels and patterns of seedling establishment for the two case studies described in Box 2. For both case studies, we apply the Janzen–Connell hypothesis to predict that the probability of seedling establishment increases with distance from the source tree (Comita et al., 2014; Connell, 1971; Janzen, 1970). (a) Japanese macaques of different social statuses differ in seed-dispersal efficacy during non-masting years. Because subordinate macaques provide higher-quality dispersal (i.e. lower rates of seed mastication), we predict that the probability of seedling establishment will be greater for seeds dispersed by subordinates than those dispersed by dominant individuals. (b) Flying foxes that differ in social status differ in seed-dispersal efficacy. We expect that the probability of seedling establishment remains low when seeds are dispersed by dominant individuals because those seeds are dispersed directly below the source tree

Box 2 Case studies where social status affects seed-dispersal effectiveness

A few case studies have demonstrated that the effects of social status on individual behavior lead to predictable patterns in intraspecific variation in seed-dispersal effectiveness. Importantly, these case studies also illustrate that increases in the availability of resources for subordinate individuals (e.g., masting events or population decline) can lead to seed-dispersal limitation when subordinates no longer require fruit as a secondary resource or rely on thieving intruder tactics. We provide predicted seed-dispersal kernels and patterns of seedling establishment for both case studies (Figure 2).

JAPANESE MACAQUES (*MACACA FUSCATA*)

Japanese macaques are omnivorous primates that prefer nuts over fleshy fruit (Tsuji & Takatsuki, 2012). Tsuji et al. (2020) found that in a year when the preferred nut resource was low in abundance, high-ranking individuals defended this resource, forcing low-ranking individuals to consume and disperse fleshy fruit. Low-ranking individuals also provided higher-quality seed dispersal as subordinates had lower rates of seed mastication (Figure 2a; Tsuji et al., 2020). In contrast, during the masting year for nuts, there were no differences between social ranks in seed-dispersal effectiveness (Tsuji et al., 2020). Because subordinate individuals had greater access to nuts, they consumed and dispersed less fleshy fruit (Tsuji et al., 2020). Dominant individuals continued to be low-quantity seed dispersers, but the quality of seed dispersal increased during the mast year due to lower rates of seed mastication (Tsuji et al., 2020).

FLYING FOX (*PTEROPUS TONGANUS*)

Dominant flying foxes defend fruiting trees as territories, repelling subordinate intruders that seize fruit to consume in a distant location (Banack & Grant, 2002; McConkey & Drake, 2006; Nelson, 1965; Trewhella et al., 2001; Wiles & Johnson, 2004). Because dominant, territorial individuals rarely move away from the trees they defend, most seeds dispersed by these individuals fall below the source tree (McConkey & Drake, 2006; Richards, 1990). Because subordinate individuals move seeds further distances from the source tree, these individuals provide higher-quality and long-distance seed dispersal (Figure 2b; McConkey & Drake, 2006; Richards, 1990)). However, in order for subordinate individuals to exhibit this intruder strategy, all fruiting trees need to be saturated with dominant, territorial individuals (McConkey & Drake, 2006). McConkey et al. (2006) show that once flying fox densities fell below a certain threshold, trees were no longer saturated by dominant individuals, allowing most individuals to remain in their trees, reducing the frequency of intruding behaviours and rates of seed dispersal away from defended trees.

(Figure 1). Studies that not only estimate seed dispersal but also measure post-dispersal seed fate (i.e., seed predation and recruitment) at deposition sites will provide greater clarity on how the quality of seed dispersal varies between individuals of different social statuses. For example, past work shows that seed deposition in coyote scat increases seed survival for rodent-preferred seeds but decreases seed survival for arthropod-preferred seeds due to the contrasting effects of mesopredator scat on rodents (aversion) and arthropods (attraction; Bartel & Orrock, 2021). Hence, if dominant individuals deposit seeds in habitats with different granivore communities than the habitats in which subordinates deposit seeds, then the probability of post-dispersal seed survival may drastically differ. This contrast may be most evident in group-living canids, like coyotes, where dominant individuals spend more time maintaining territory boundaries, often through scent-marking and scat deposition, than subordinate individuals (Gese, 2001). Because territory boundaries often fall along habitat edges, including roads and trails, seed fate may differ among dominant- and subordinate-dispersed seeds if granivores either avoid or prefer edges.

Multilevel societies may represent interesting cases where the utility of our framework depends upon the level of consideration. We anticipate that our framework may be less useful in predicting individual-level variation in seed-dispersal effectiveness in multilevel societies where individuals consistently travel in groups because individual movement and access to resources may be more strongly affected by the dominance of the group, relative to other groups, than an individual's rank within the group (Dunbar, 1988; Ward & Webster, 2016c). However, our framework may be useful for predicting group-level variation in seed-dispersal efficacy in multilevel societies. For example, African elephants (*Loxodonta africana*) are thought to be "megagardeners" of landscapes by dispersing seeds over long distances in nutrient-rich

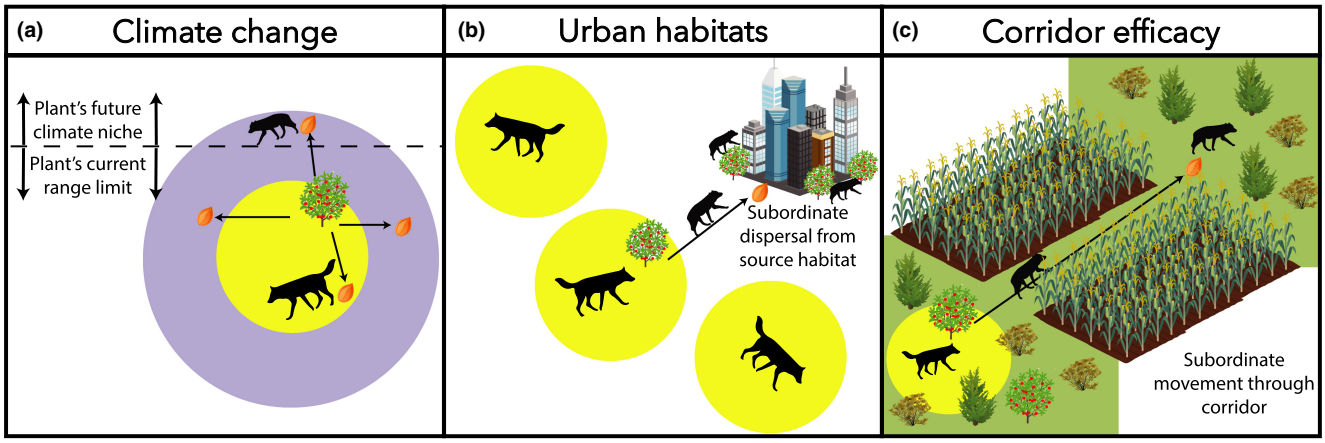


FIGURE 3 The effects of social status on seed dispersal may have important implications for the movement and recruitment of plants in the Anthropocene. (a) Because subordinate individuals typically have larger home ranges and disperse beyond the territories of conspecifics, subordinate individuals are more likely to provide long-distance seed-dispersal services. Because long-distance seed dispersal is critical for many plants to expand range boundaries, subordinate individuals may facilitate plant movement to track changing climate. (b) Subordinate individuals are more likely to disperse into urban habitats. Subordinates may, therefore, facilitate plant species dispersal and persistence in urban habitats. (c) Because subordinate individuals have larger home ranges and are more likely to disperse beyond current conspecific territories, they may be more likely to use corridors. The movement of subordinate individuals through corridors likely facilitates plant movement through corridors, promoting plant establishment in otherwise isolated habitat patches

dung (Campos-Arceiz & Blake, 2011). African elephants form multilevel societies in which dominant groups disproportionately use preferred habitats and move shorter distances than subordinate groups during the dry season when resources are limited (Wittemyer et al., 2007). It is therefore likely that subordinate groups move seeds longer distances than dominant groups due to this difference in movement. Because elephant groups also differ in habitat use during the dry season, the quality of seed dispersal by dominant and subordinate groups is also likely to vary depending on whether the preferred habitats (used by dominant groups) are high-quality or low-quality deposition sites for plant recruitment.

An individual's efficacy as a seed-dispersal agent may change over its lifetime if social status changes over a lifetime. The capacity for subordinate individuals to disperse seeds longer distances and into a greater variety of habitats than dominant individuals is perhaps most evident in systems where subordinate juveniles disperse from natal territories defended by dominant breeding adults (Blitzer et al., 2012). Recent work on Sardinian warblers (*Sylvia melanocephalahas*) illustrates that juveniles dispersing from natal territories can provide functional connectivity for plants between isolated habitats by dispersing seeds through the matrix (González-Varo et al., 2019). Hence, the subordinate social status of juveniles in natal territories can be an important mechanism by which seeds may be dispersed long distances and into a greater diversity of habitats than the habitats used by adults (Blitzer et al., 2012; González-Varo et al., 2019). Social dominance in grizzly bear (*Ursus arctos horribilis*) populations is typically a result of individual size (larger bears are dominant over smaller bears) and reproductive status (females with cubs are subordinate to single males; Ben-David et al., 2004; Gende & Quinn, 2004). Because individual social status affects bear diet and space use (Box 1), juvenile males are likely to become less effective seed-dispersal agents over their lifetime, and females are likely to be most effective seed-dispersal agents during their lifetime when they are rearing cubs. Crocodilian species (order Crocodylia) can also consume large quantities of fleshy fruit, yet their role as agents of seed dispersal is largely unappreciated (Platt et al., 2013). Some crocodile populations can have distinct dominance hierarchies (Garrick & Lang, 2020; Platt et al., 2013; Tucker et al., 1998), and individual social status, which is generally a function of ontogeny and territoriality, can affect movement patterns that may then generate predictable intraspecific variation in seed dispersal (Platt et al., 2013). For example, non-territorial subadult Nile crocodiles (*Crocodylus niloticus*) exhibit the highest range of movement than all other social classes because they do not maintain distinct home ranges during this life stage (Hutton, 1989). Long-distance movement by socially subordinate subadults that are forced to disperse from natal habitats due to intraspecific competition has also been documented in Australian freshwater crocodiles (*Crocodylus johnstoni*; Tucker et al., 1998). It is, therefore, possible that socially subordinate, subadult crocodilians provide uniquely long seed-dispersal services.

The capacity for an individual's efficacy as a seed-dispersal agent to rapidly change raises a clear distinction between the effects of social status and personality on seed dispersal. While definitions of animal personalities are often context- or system-specific, personality is most broadly defined as individual differences in behaviour that are consistent across time and/or contexts (Dall et al., 2004; Stamps & Groothuis, 2010). In

contrast, an individual's social status has the capacity to change across time or context, particularly as a result of changes in the individual's social environment. Although individual personality traits can sometimes be correlated with social dominance (Briffa et al., 2015), personality and social dominance are not related in many animal societies (Devost et al., 2016; Favati et al., 2013; Funghi et al., 2015). Dominance is the product of myriad environmental factors (e.g., relative size, relative age, reproductive status, maternal rank, social alliances; Devost et al., 2016; Favati et al., 2013; Funghi et al., 2015; Ilany et al., 2021; Strauss & Holekamp, 2019), but personality is by definition consistent across time and context, although it may develop in response to individual experience (Stamps & Groothuis, 2010). Hence, behavioural tendencies that are a result of personality should remain consistent over short timespans, but any changes to an individual's social environment that lead to a rapid change in social status are expected to rapidly change individual behaviour and efficacy as a seed-dispersal agent.

CONSEQUENCES OF GLOBAL CHANGE FOR SOCIALLY MEDIATED SEED DISPERSAL

Our framework illustrates that in many systems where fruit is a supplemental resource for animals (e.g. carnivores and folivores), subordinate individuals are likely to be the most effective seed-dispersal agents, and thus may be critical for understanding patterns in plant populations in the Anthropocene. First, because subordinate individuals have less restricted home ranges and are more likely to disperse to locations outside of the established territories of conspecifics (e.g., subadults dispersing outside of natal territories; Aycrigg & Porter, 1997; Dorning & Harris, 2017; Henry et al., 2005; Kamler et al., 2019), subordinate individuals may be more likely to provide long-distance seed-dispersal events (e.g. González-Varo et al., 2019). Long-distance seed dispersal is critical for plant species range expansion to track changing climates (Cain et al., 2000; Corlett & Westcott, 2013; Dyer, 1995; Fricke et al., 2022; González-Varo et al., 2017, 2021; Naoe et al., 2016, 2019). Hence, subordinate individuals may facilitate range expansions that allow plant species to track changing climates (Figure 3a). Recent work by Fricke et al. (2022) revealed that the potential for long-distance seed dispersal to track climate is particularly limited in temperate regions and landscapes with minimal topographic complexity. Subordinate individuals that move long distances may be extremely important for providing rare, climate-tracking seed-dispersal events in these locations. Second, because subordinate individuals are more likely to use less-preferred habitats (Aycrigg & Porter, 1997; González-Varo et al., 2019; Ward et al., 2018; Wittemyer et al., 2007), and urban habitats are often demographic sinks (Lamb et al., 2017, 2020; Vierling, 2000), subordinate individuals may be more likely to transport seeds into urban habitats, playing a potentially unappreciated role in promoting the spread and persistence of some plant populations in urban landscapes (Figure 3b). Differences in movement across fragmented landscapes due to social status may also have important, yet unappreciated implications for the efficacy of conservation corridors (i.e., thin strips of habitat connecting otherwise isolated patches). While corridors have been shown to increase plant species diversity, including animal-dispersed plants (Damschen et al., 2006, 2019), there is limited knowledge of how an animal's social status affects its propensity to move through corridors (but see Box 1 for discussion of work by Ford et al. (2017)). Because subordinate individuals typically forage in a larger number of patches in a landscape and are more likely to disperse from natal habitats (González-Varo et al., 2019), we predict that subordinate individuals may disproportionately contribute to seed movement through corridors and the consequent benefits of corridors to plant diversity (Figure 3c). Initiatives to restore plant communities through corridor implementation may, therefore, require wildlife management that maintains or restores social structure in animal populations. Finally, if subordinate individuals have significant contributions to the quantity and spatial spread of seed dispersal, then subordinate individuals may facilitate the spread of invasive plants. Our framework provides a means to begin exploring (and mitigating) these effects. Socially mediated dispersal may also provide a lens through which to examine novel interactions caused by invasive plants: recent work highlights how invasive plants affect animal behaviour, including foraging behaviour of animals that disperse plants (Fletcher et al., 2019; Stewart et al., 2021; Traveset & Richardson, 2014), and it remains unknown whether these shifts in animal behaviour can be predicted based on social status.

Our framework also highlights how environmental changes that modify animal social structure and behaviour may have indirect consequences for plant populations through changes in seed-dispersal effectiveness. For example, rank-dependent differences in diet and space use often only occur during seasons when the preferred resource is limited and can be defended by dominant individuals (Pazol & Cords, 2005; Tsuji et al., 2020; Wittemyer et al., 2007). Events that cause an overabundance of a preferred resource (e.g., masting, human subsidies or biological invasions) could, therefore, lead to a cryptic function loss of seed dispersal by subordinates (McConkey & O'Farrill, 2015; Box 2). It is generally appreciated that provisioning of anthropogenic resources can lead to declines in seed dispersal by reducing fruit removal rates by wildlife (Sengupta et al., 2021), but there is limited understanding of how changes in social behaviour due to provisioning may be a mechanism by which seed dispersal is affected by anthropogenic resources. It has been shown that animal social network

structure is relaxed near anthropogenic habitats (Belton et al., 2018; Morrow et al., 2019), indicating that a potential mechanism by which anthropogenic resources may reduce seed-dispersal services is when high-quality foods are no longer defended by dominant individuals. Although it is appreciated that animal species extinction can lead to catastrophic losses in plant biomass due to seed-dispersal limitation (Peres et al., 2016), we posit that shifts in animal social behaviour may have similar deleterious effects on plant biomass. For example, territorial defense of fruit-bearing trees by mistle thrushes (*T. viscivorus*) is positively correlated with population density. Intraspecific variation in the quantity and distance of seed dispersal in thrushes may, therefore, be minimal in low-density populations. Importantly, in the absence of territory defense, territory intruders would no longer disperse seeds far distances from defended trees. A study by McConkey and Drake (2006) on seed dispersal by flying foxes also illustrated that seed-dispersal services may be lost when animal population densities fall below a threshold for density-dependent behaviours that lead to seed dispersal (Box 2). Consequently, the functional role of animals as seed-dispersal agents can be lost in the early stages of species decline when social behaviours diminish, long before species become rare (McConkey & Drake, 2006; McConkey & O'Farrill, 2015, 2016). Alternatively, in social systems where aggressive interactions among individuals disrupt behaviours that facilitate seed dispersal, changes in the environment that alter the frequency of aggressive interactions may indirectly affect seed-dispersal kernels. For example, island scrub jays (*Aphelocoma insularis*) are scatter hoarders that secondarily disperse seeds by caching seeds in the soil; however, jays will stop caching seeds when rates of territorial aggression are high (Pesendorfer et al., 2016). It is, therefore, possible that increases in population density in this context may indirectly decrease the quantity and distance of seeds dispersed by increasing the frequency of aggressive behaviours. Finally, while it is known that harvesting frugivorous animals causes seed-dispersal limitation (Fricke et al., 2022; Peres et al., 2016), we posit that selective harvesting of dominant individuals may also lead to seed-dispersal limitation (Box 1). By removing dominant males or matriarchs from populations, selective harvesting can disrupt social systems (Milner et al., 2007), which may lead to reductions in seed-dispersal efficacy by subordinate individuals if dominant individuals are no longer able to establish territories or defend preferred resources.

It is unclear if changes in plant communities and the distribution of resources may indirectly affect seed dispersal by changing the identity and defense of resources used by social animals. For example, human disturbances may modify the types of resources available, which may alter consumer resource preferences (e.g. dominant individuals that used to defend a patchy resource switch to consuming agricultural crops) and the economics of resource defense. It is possible that in cases where consumer preference does not change, the ability or profitability of defending resources may be diminished, which may change the quantity of seeds dispersed by subordinate individuals. For example, defense of fruit-bearing trees by territorial fieldfares (*T. pilaris*) against non-territorial, intruder fieldfares is dependent on fruit density (Skórka et al., 2006). Because the frequency of territorial behaviour in fieldfare populations is positively correlated with fruit density (Skórka et al., 2006), intraspecific variation in the quantity and distance of seed dispersal in fieldfares may be minimal in years with low fruit yield and poorly explained by social status. Importantly, with the absence of territorial fieldfares, there would also be an absence of territory intruders that may disperse seeds longer distances from the source trees. Hence, seed-dispersal kernels may be substantially shorter during years of low fruit yield due to the effects of resource density on animal social behaviour. Human activity may also affect the ability for animals to defend resources. Recent works suggests that carnivores abandon carcasses more quickly in the presence of human activity (Suraci et al., 2019), indicating that spatially clumped resources may be less defended by dominant individuals when located near human activity, possibly leading to greater access to preferred resources for subordinate individuals. Consequently, the quantity of seed dispersed by subordinate individuals may be substantially reduced in human-disturbed landscapes.

FUTURE DIRECTIONS

While centuries of research have been devoted to characterising and understanding animal social behaviour, there is a surprisingly limited amount of knowledge of how social behaviours affect trophic interactions to generate patterns in communities (González-Varo et al., 2019; Jadeja et al., 2013; McConkey & Drake, 2006; Tsuji et al., 2020). Because animal social status can predictably affect individual resource access and movement, investigating how animal social behaviours contribute to intraspecific variation in seed-dispersal effectiveness may explain some of the unresolved variation in seed dispersal and plant recruitment. There is an important lacuna in non-primate systems for understanding how social status may explain intraspecific variation in diet and space use, and consequently seed-dispersal effectiveness. Although a few studies show that social status explains individual diet composition in some potential seed-dispersing vertebrates (e.g., pampas foxes and pronghorn; Castillo et al., 2011; Dennehy, 2001), there is limited knowledge of how it may explain the well-documented dietary variation in omnivorous species where social status is known to determine resource access, such as many carnivore species (Box 1). Because this current lacuna is likely

TABLE 1 We present example experimental designs to test the general hypothesis that individual social status predicts intraspecific variation in seed-dispersal effectiveness using non-invasive methods that could be adopted for a wide variety of wildlife species, particularly for populations unhabituated to human observers (see Quintero et al. (2021) for a thorough review of techniques used for monitoring endozoochorous seed dispersal)

Approach	Social status estimation	Seed dispersal measurements
Experimental: Wild populations	Social interactions: • Remote cameras to video-record behaviour of individuals in social context at foraging stations • Each station has two food items: primary resource (e.g. carrion) and secondary resource (fruit) • Direction of aggressive/submissive behaviours indicates relative dominance among individuals in a dyad or group • Food item selection by solitary individuals confirms a preference for primary resource and role of social interactions in frugivory Link individual behaviour to scat collection: • Food items are tagged with fine glitter or fluorescent dye (unique colour for each station) • Hair snags near each food item to capture DNA samples to ID individual genotypes	Dispersal distance: • Presence/colour of glitter or dye in scat indicates distance and direction of movement from station Quantity of seeds dispersed: • Count number of seeds per scat deposit • Germination trials to estimate # viable seeds per scat • Sequence DNA from scat to link individual genotypes from scat and feeding station assay Quality of seed dispersal: • Examine post-dispersal seed fate and quantify rates of seed predation (see Bartel & Orrock, 2021 for seed-removal tray design) and seedling establishment in microhabitats where scat is found
Experimental: Captive populations	• Human observers record direction of aggressive/submissive behaviours to estimate each captive group's dominance hierarchy • Each group is given two food items: primary resource (e.g. carrion) and secondary resource (fruiting shrubs)	Dispersal distance: • Observations of individual gut retention times can be used with published estimates of movement distances in wild populations to estimate potential dispersal distance Quantity of seeds dispersed: • Count number of seeds per scat deposit per individual • Germination trials to estimate seed viability
Observational: Remote cameras	• Remote cameras to video-record behaviour of individuals in social context at primary resources (e.g., carrion or fruiting trees) and secondary resources (e.g., fruiting shrubs) • Direction of aggressive/submissive behaviours indicates relative dominance among individuals in a dyad or group • Individuals may be distinguished either visually in photos or with radio-collars	Dispersal distance: • Published estimates of gut retention times and movement distances can be used to estimate potential dispersal distance Quantity of seeds dispersed: • Visually estimated through video recordings at fruit sources (# of visits and # of seeds consumed per visit)
Observational: Molecular analyses	Extensive scat collection may be done in systems where social status carries a molecular signature. Identify individuals through genetic analysis of scat. The following molecular approaches may be used estimate individual social status: • Faecal glucocorticoid concentration is related to dominance in some cooperative breeding species (Creel, 2001) • Reproductive hormone concentrations may be used in systems where reproductive status affects dominance • Genetic analyses to identify sex may be used when sex affects dominance • Average mass of scat per individual may provide estimation of individual size when size affects dominance	Quantity of seeds dispersed: • Count number of seeds per scat deposit • Germination trials to estimate # viable seeds per scat Quality of seed dispersal: • Examine post-dispersal seed fate and quantify rates of seed predation and seedling establishment in microhabitats where scat is found

due to the difficulty of tracking both seed fate and the behaviours of cryptic animals, we suggest methods for systems where animal behaviour and seed fate cannot be measured by direct human observation of wild animals (Table 1). Our framework also highlights that individual social status may play an unappreciated role in determining post-dispersal seed survival and recruitment when individuals that differ in social status use different habitat types. We, therefore, strongly suggest that future research measuring individual behaviour, social status and seed movement also evaluate the quality of seed-deposition sites by measuring rates of post-dispersal seed predation and seedling establishment (Table 1). In addition to the example

study designs that we provide in Table 1 to apply our framework, we also encourage researchers to refer to a recent review by Quintero et al. (2021) that thoroughly describes the wide array of techniques for monitoring endozoochorous seed dispersal. We predict that our framework will be most important in systems where plant species are dispersal limited, animal social status affects individual diet and movement, and fleshy fruit is an essential dietary supplement for subordinate individuals (e.g. carnivore and folivore populations). Understanding how social status affects seed dispersal may be most critical in systems where animal social structure is modified or destabilised, illuminating cryptic hotspots of seed dispersal loss.

ACKNOWLEDGEMENTS

We thank K.B. Strier, J. Kraus, C. Zirbel, C. Keller, M. Fuka, A. Weidemann, J. Drake, and three anonymous reviewers for thoughtful discussion and helpful comments on the manuscript. This work was supported by NSF DEB 2042211, USDA NIFA 2021-67019-33427, and the Albert R. and Alma Shadle Fellowship from the American Society of Mammalogists.

AUTHOR CONTRIBUTIONS

SLB and JLO developed the conceptual framework. SLB prepared the first draft, and both authors contributed substantially to revisions.

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/ele.13988.

DATA AVAILABILITY STATEMENT

No data were used in this manuscript.

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How to cite this article: Bartel, SL, Orrock, JL (2022) The important role of animal social status in vertebrate seed dispersal. *Ecology Letters*, 25, 1094–1109. https://doi.org/10.1111/ele.13988