

## REVIEW

Functional Ecology



# Animal personalities and seed dispersal: A conceptual review

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## Abstract

1. Consistent individual tendencies in behaviour, or behavioural types, are likely to impact the dynamics and outcomes of animal-mediated seed dispersal. We review the extant literature on this issue and outline a conceptual overview to guide this emerging field. We provide an overview of possible ways in which behavioural types can affect animal-mediated seed dispersal. We summarize theoretical mechanisms linking behavioural types with seed dispersal outcomes and review how behavioural types might affect each stage of seed dispersal, beginning with fruit encounter and harvest, and ending with events that take place after seed deposition.
2. Since behavioural types involve correlations among different behaviours (i.e. behavioural syndromes), they can generate unexpected associations between different decisions that are involved in seed dispersal, with conflicting (or reinforcing) effects on different stages of seed dispersal. Thus, we draw particular attention to trade-offs faced by seeds dispersed by individuals with different behavioural tendencies. We also note that since seed dispersal is a multiplicative process with different stages, disperser behavioural types that provide moderately efficient dispersal at each stage will be better for plants than behavioural types that are very efficient at some steps, but inefficient on others. Finally, we provide testable predictions on the links between behavioural types and characteristics of seed dispersal, including, for example, influences on the probability of seed harvest, dispersal distance, deposition sites and condition of dispersed seeds.
3. We argue that investigating the links between behavioural types and animal-mediated seed dispersal will provide a better mechanistic understanding of seed dispersal and plant regeneration.

## KEYWORDS

animal personalities, endozoochory, frugivory, individual variation, scatterhoarding, seed dispersal effectiveness, synzoochory

## 1 | INTRODUCTION

Seed dispersal is commonly provided by foraging frugivores or scatterhoarding animals (Gómez, Schupp, & Jordano, 2019; Herrera, 2002; Jordano, 2000). Their actions can impact dynamics and genetic structure of plant populations, composition and species richness of plant communities, and a

diversity of evolutionary pressures acting on plants (Elwood, Lichti, Fitzsimmons, & Dagleish, 2018; Gelmi-Candusso, Heymann, & Heer, 2017; Rogers et al., 2017). Therefore, mechanisms underlying patterns and outcomes of animal-mediated seed dispersal generate intense interest (Lichti, Steele, & Swihart, 2017; Schupp, Jordano, & Gómez, 2017; Zwolak & Crone, 2012). However, researchers investigating animal-mediated seed dispersal typically

**TABLE 1** Predicted effects of particular personality traits (divided into five major categories: Réale et al., 2007) on different stages of seed dispersal. Predictions are for animals that score high in a given category; for those that score low, we predict the opposite effect. The categories are not independent of each other (e.g. proactive individuals generally score high for all of these traits and reactive individuals score low)

	Frugivores and Scatterhoarders			Scatterhoarders		
	Encountering fruits	Decision to harvest versus ignore	Dispersal distance	Seed condition	Deposition site	Partial seed consumption
Aggressiveness		More likely to restrict access to fruiting plants	Less likely to carry seeds away for consumption			
Sociability		More likely to join other foraging individuals		Seeds more aggregated		
Boldness	More likely in risky situations	More likely to forage in risky situations	Higher tolerance of predation risk leads to lower giving-up density, which can translate into shorter dispersal; less likely to carry seeds away for consumption	More likely to deposit seeds in open habitats	Less likely due to lower giving-up density	More likely to eat (rather than cache) due to lower survival and residual reproductive value
Activity	More likely	More likely to forage because of higher energy needs; more likely to specialize on higher-quality fruits	Lower gut retention time; lower giving-up density (thus potentially shorter dispersal) because of higher energy needs	Higher seed viability due to lower gut retention time (but too short might not break dormancy)	Less likely due to higher energy needs	More likely to eat (rather than cache) due to high energy needs
Exploration	Higher chance for obvious fruit; lower for less obvious ones	More likely to forage on novel fruits; more likely to specialize on higher-quality fruits; less affected by spacing of food patches	More likely to transport seeds far from mother plants			Higher chance of pilferage of obvious seeds; lower of less obvious seeds

focus on estimating average dispersal services provided by a given animal species. In the process, individuals that possess different, unique combinations of traits are averaged out of existence (Bennett, 1987; Violle et al., 2012).

Calls for appreciating the importance of individual variation in ecology are not new (Leslie, 1945; Łomnicki, 1978), but have been addressed most frequently in the context of sex-, size- and age-related variation (reviewed by Bolnick et al., 2011; Violle et al., 2012; Zwolak, 2018). Consistent inter-individual variation in behaviour (e.g. boldness or aggressiveness) is a less obvious trait that only recently has gained widespread attention of researchers (Réale, Reader, Sol, McDougall, & Dingemanse, 2007; Sih, Bell, & Johnson, 2004; Sih, Bell, Johnson, & Ziemba, 2004; Wolf & Weissing, 2012). Their findings challenge the assumption that individual variation in behaviour merely represents non-adaptive deviations from an adaptive mean. Instead, animal behaviour appears to be optimized within constraints that vary from individual to individual (Dall, Houston, & McNamara, 2004). Moreover, various behavioural tendencies often covary in 'behavioural syndromes' (Sih, Bell, & Johnson, 2004; Sih, Bell, Johnson, & Ziemba, 2004), and can be associated with physiological and cognitive differences (Mathot, Dingemanse, & Nakagawa, 2019; Sih & Del Giudice, 2012) or variable life-history strategies (Réale et al., 2010). Within the syndromes, which are described at population or species level, individuals display 'behavioural type' (e.g. more active vs. less active behavioural types: Sih, Bell, & Johnson, 2004; Sih, Bell, Johnson, & Ziemba, 2004), here also referred to simply as 'personality'. To the extent that generalizations are possible, animals that are highly active and exploratory also tend to be neophilic, aggressive in contacts with conspecifics and bold in the presence of predators (but see Dougherty & Guillelte, 2018). In contrast, animals that are shy, neophobic and cautious are typically characterized by relatively low levels of aggression, activity and exploratory tendency. The former are often referred to as 'proactive' and the latter as 'reactive' behavioural types (Koolhaas, De Boer, Buwalda, & Van Reenen, 2007). Proactive animals are thought to have a high resource acquisition rate, but relatively low survival ('high risk-high reward' strategy) and they tend to invest in current rather than future reproduction. Reactive individuals exhibit a lower rate of resource acquisition but higher survival, investing more in future than current reproduction (Montiglio, Garant, Bergeron, Messier, & Réale, 2014; Nakayama, Rapp, & Arlinghaus, 2017; Réale et al., 2010; Wolf, Van Doorn, Leimar, & Weissing, 2007, but see Moiron, Laskowski, & Niemelä, 2020).

An accumulating body of research also demonstrates that these behavioural differences have direct ecological impacts (Sih, Cote, Evans, Fogarty, & Pruitt, 2012). However, empirical studies on the potential impact of behavioural types on seed dispersal are just beginning to emerge. Here we provide an overview and critique of that literature. Our primary goal is to develop a general framework and specific recommendations to guide future work on the role of individual variation in animal-mediated seed dispersal (Zwolak, 2018).

Our focus is on seed dispersal provided by vertebrate frugivores ('endozoochory') and scatterhoarding granivores ('synzoochory'),

but many points we raise here are also applicable to other forms of seed dispersal by animals, such as inadvertent attachment of seeds to the body surface ('epizoochory'). We begin with a brief synopsis of seed dispersal by frugivores and scatterhoarders. We then outline ways in which decisions made by dispersers of different behavioural types might affect seed fate, propose specific mechanisms that are likely to connect behavioural types and seed dispersal outcomes, and provide predictions to be tested in future studies (Table 1).

## 2 | SEED DISPERSAL BY FRUGIVORES

Most frugivores feed on fleshy fruits, eating pulp and discarding, regurgitating or defecating seeds, often at places that are away from the parent plant. Therefore, frugivore-plant interactions are considered 'food for movement' mutualisms (Herrera, 2002). Accordingly, Howe (1986) argued that the most important characteristic of many frugivores is the 'predilection for sitting in place, or choosing a place in the open or in the shade to sit while processing seeds'. While in many cases this might be true, there are also other steps along the route from fruit encounter to seed deposition that potentially affect the strength and outcome of a given plant-frugivore interaction. We briefly cover them below.

### 2.1 | Encountering fruits

To disperse seeds, frugivores must first encounter fruits. The probability of finding fruits is influenced by the location and size of the frugivore's home range, by its decisions about where and when to forage, and by its ability to detect fruits by visual cues, smells or sounds produced by falling fruits or feeding animals (Corlett, 2011).

### 2.2 | Decision to harvest or ignore

When fruits are encountered, the frugivore must decide whether to forage (and if so, for how long) or to move on in the search for better opportunities. Animals might reject fruits for many reasons: foraging in a given place or time might be too risky, the animal might be satiated, handling or transportation costs might be too high, the fruits might be deemed low quality, or not recognized as edible. Furthermore, animals must determine which fruits to choose from a patch. Size, ripeness and infestation by pests and diseases are important factors that influence the perceived quality of fruits (García, Zamora, Gómez, & Hódar, 1999). The decisions to harvest versus ignore and when to quit foraging on encountered fruits is crucial for plants because seeds in unharvested fruit often have drastically reduced chances of germinating and producing seedlings (Jaganathan, Yule, & Liu, 2016; Rogers et al., 2017; Zwolak & Crone, 2012). From the plant perspective, unharvested fruits often are a wasted investment.

## 2.3 | Dispersal distance

Harvested fruits are often carried away, in mouths, paws or stomachs, and deposited at a varying distance from the parent plant (Anderson, Nuttle, Saldaña Rojas, Pendergast, & Flecker, 2011; Lima & Valone, 1986; Soons, Van Der Vlugt, Van Lith, Heil, & Klaassen, 2008). Such dispersal helps offspring escape negative density dependence that is often associated with parent plants (Jansen, Bongers, & Van Der Meer, 2008; Terborgh et al., 2008) and increases the chances of colonizing ephemeral habitats (Brodie, Helmy, Brockelman, & Maron, 2009; Soons et al., 2008). Thus, longer seed dispersal distances are usually considered advantageous. However, distance of seed dispersal does not always translate into benefits for plant recruitment, and even when it does, the relationship can be quite complex (discussed in Schupp, Jordano, & Gómez, 2010). When habitat suitability is spatially correlated (e.g. when the parent's success is an indicator of local habitat suitability), increasing distance of seed dispersal might reduce chances of successful recruitment (Baythavong, Stanton, & Rice, 2009; Condit, Engelbrecht, Pino, Pérez, & Turner, 2013). Moreover, contagious dispersal (when some sites receive few dispersed seeds while others serve as dispersal foci) means that even long-distance dispersal might put seeds in places with intense competition or seed predation (Kwit, Levey, & Greenberg, 2004; Razafindratsima & Dunham, 2016; Wright, Calderón, Hernández, Detto, & Jansen, 2016).

## 2.4 | Seed condition after fruit processing

Seed condition after dispersal is affected by the seed-processing behaviour of a frugivore and by traits of its digestive system (Jordano, 2000). For example, mashing or masticating fruits can result in cracking seeds. Similarly, long retention times of seeds within the gut might result in digestive damage (Traveset, Robertson, & Rodríguez-Pérez, 2007). On the other hand, seed scarification and pulp removal are often necessary to stimulate seed germination (Fedriani, Żywiec, & Delibes, 2012; Traveset et al., 2007). Moreover, gut passage might remove seed pathogens and substances that attract seed predators (Fedriani et al., 2012; Fricke et al., 2013).

## 2.5 | Deposition site

The final fate of the seeds (and ultimately their reproductive fitness) depends not only on their condition after handling or gut passage but also on environmental conditions at the place where the seeds are dropped, defecated or regurgitated (Jordano, 2000). The phenomenon when dispersed seeds arrive disproportionately in particularly favourable sites is known as 'directed dispersal' (Wenny, 2001). The quality of deposition sites is influenced by patterns of frugivore movements, by their habitat choices and by patterns of seed aggregations, as seeds can be deposited in a scattered or clumped fashion

(Howe, 1989). Size and species composition of these aggregations affect the risk of seed predation, strength of future density dependence and competitive or allelopathic interactions experienced by plants (Spiegel & Nathan, 2010; Traveset et al., 2007). In some cases, effects of seed aggregation are more important than the (density-independent) quality of the site where seeds are deposited (Kwit et al., 2004; Salazar, Kelm, & Marquis, 2013; Spiegel & Nathan, 2010; but see Sugiyama, Comita, Masaki, Condit, & Hubbell, 2018 for a counter-example).

In summary, from the plant's view, an efficient seed disperser ingests many seeds and deposits them in good condition and not overly crowded in microsites that provide high potential for germination, survival and growth (Schupp et al., 2010, 2017).

## 3 | SEED DISPERSAL BY SCATTERHOARDERS

Foraging behaviours of frugivores and scatterhoarding granivores are similar in many respects; Vander Wall and Beck (2012) provide a detailed comparison. In contrast to frugivores, however, scatterhoarders feed directly on seeds, dispersing them in the process of caching surplus seeds for consumption when food is scarce or foraging conditions are unfavourable (Vander Wall, 1990). Since scatterhoarders act both as seed dispersers and seed predators, many plant–scatterhoarder interactions are highly conditional and inherently a balance between mutualism and antagonism (Bogdziewicz, Crone, & Zwolak, 2019; Gómez et al., 2019; Zwolak & Crone, 2012). Even when seeds are cached rather than immediately eaten, the interests of seeds and seed-caching animals remain in conflict because only uneaten seeds have a chance of germination, but scatterhoarders cache seeds precisely to consume them in the future (see e.g. Neuschulz, Mueller, Bollmann, Gugerli, & Böhning-Gaese, 2015). Below, we describe steps in the seed dispersal process that are typical in scatterhoarding, but are usually absent in frugivory.

### 3.1 | Partial seed consumption

Not all seeds that are eaten by scatterhoarders die. Some are only partially consumed and retain the ability to germinate and produce seedlings (Loayza, Carvajal, García-Guzmán, Gutierrez, & Squeo, 2014; Steele, Knowles, Bridle, & Simms, 1993; Yi, Wang, Liu, Liu, & Zhang, 2015). This is thought to happen most often with large seeds that are capable of satiating granivores (Perea, San Miguel, & Gil, 2011).

### 3.2 | Decision to eat versus cache seeds, and the fate of cached seeds

'Scatterhoarding' means storing seeds in many concealed but undefended locations, each with one or a few seeds (Lichti et al., 2017; Vander Wall, 1990). Some granivores use a mixed strategy of

scatterhoarding and larderhoarding (caching many food items in one, large, defended cache: Vander Wall, 1990). Typically, scatterhoarded seeds are placed in shallow caches in topsoil, whereas larderhoarded seeds are placed in deep underground burrows, middens, tree granaries or other places where seed survival is unlikely (Vander Wall, 1990). Thus, only scatterhoarded seeds have much chance of producing seedlings and are the main focus of this review.

Seed deposition in topsoil provides numerous benefits, including protection from seed predators and from abiotic factors such as desiccation or frost (Sawaya, Goldberg, Steele, & Dalgleish, 2018; Zwolak & Crone, 2012). However, these benefits are gained only by those seeds that avoid recovery and consumption. Scatterhoarded seeds might be recovered by cache owners or by other animals (pilferers), and either eaten or cached again elsewhere. Finally, seeds that end up unrecovered, either in primary caches or after re-caching, can germinate and produce seedlings. The ultimate evolutionary and demographic outcome of plant–scatterhoarder interactions depends on the proportion of seeds that end up cached and unrecovered rather than eaten, and on the benefits for seeds of being cached (Zwolak & Crone, 2012).

In summary, a scatterhoarder most beneficial to plants harvests many seeds, places them in microsites that are safe and favourable for germination, and recovers very few or none of the caches (Zwolak & Crone, 2012).

#### 4 | MECHANISMS THAT LINK BEHAVIOURAL TYPES AND SEED DISPERSAL OUTCOMES

The above summary of seed dispersal by frugivores and scatterhoarders reveals several points at which the behaviour of seed dispersers can have major impacts on plant fitness. While it is well known that animal behaviour (foraging, movement, etc.) is important to plant dispersal, the role of behavioural types—*individual consistency* in behaviour and *consistent differences among individuals* in behaviour—in driving variation in seed dispersal is poorly known.

Hundreds of studies on a broad range of animal taxa have documented that species, populations and individuals within populations differ in their average behavioural types, including boldness, aggressiveness, exploratory tendency, general activity and sociability (reviewed in Dall et al., 2004; Réale et al., 2007; Sih, Bell, Johnson, & Ziemba, 2004). Some well-studied examples of consistent individual differences in behavioural types in potential seed dispersers include work on eastern chipmunks *Tamias striatus* (e.g. Martin & Réale, 2008; Montiglio et al., 2014), Steller's jays *Cyanocitta stelleri* (Gabriel & Black, 2010; Rockwell, Gabriel, & Black, 2012) and rhesus macaques *Macaca mulatta* (Brent et al., 2014; Hinde et al., 2015). None of these studies, however, address seed dispersal services, much less how differences in personality may drive outcomes of dispersal. Only two recent studies, both conducted on scatterhoarding rodents,

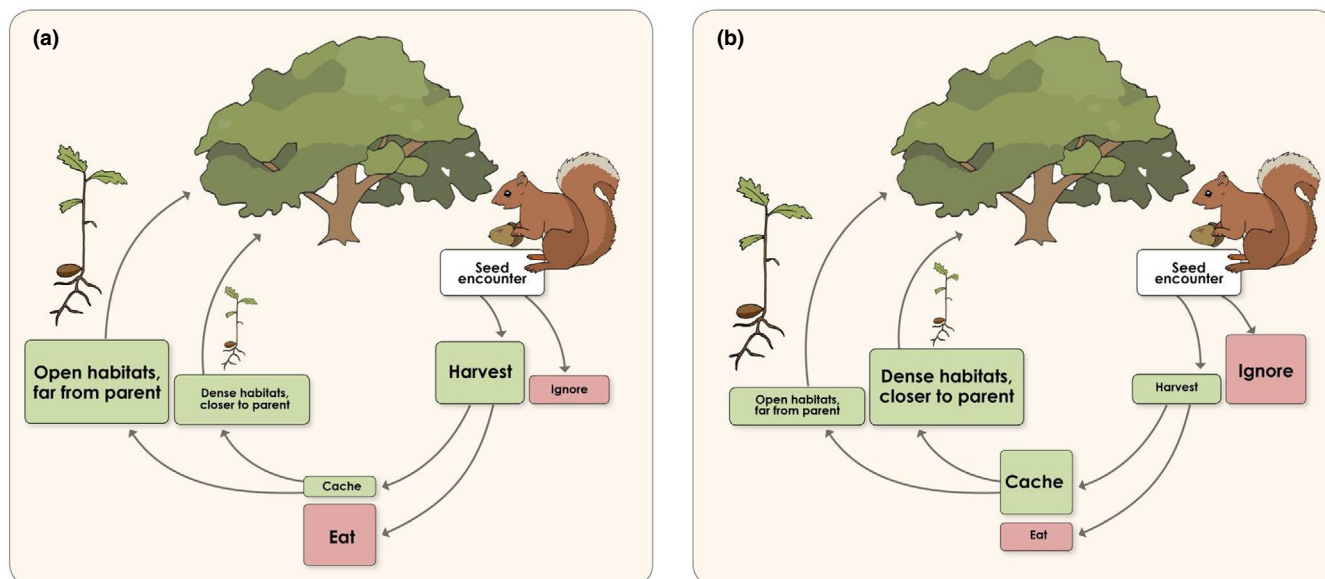
began to fill this gap (Brehm, Mortelliti, Maynard, & Zydlewski, 2019; Feldman, Ferrandiz-Rovira, Espelta, & Muñoz, 2019).

Sih et al. (2012) noted three general mechanisms underlying effects of behavioural types on ecological outcomes: (1) impacts of differences in average behavioural types at the individual, population or species level; (2) effects of within-population variation in behavioural types and (3) effects of behavioural syndromes, defined as behavioural correlations across contexts (Sih, Bell, & Johnson, 2004; Sih, Bell, Johnson, & Ziemba, 2004). Here, we outline the basic idea of these three mechanisms in the context of seed dispersal. In the following sections, we discuss each in more detail relative to the multiple stages of the seed dispersal process.

Some individuals, but also populations and species, are more social, aggressive or neophilic than others (Sih et al., 2012). Differences in average behavioural types between species or populations (mechanism 1) contribute to individual specializations of foragers (Bolnick et al., 2003; Toscano, Gownaris, Heerhartz, & Monaco, 2016), which likely lead to differences in their role in plant dispersal. Factors that affect average behavioural type can thus indirectly affect the efficiency of seed dispersal. For example, a history of high predation risk can drive the evolution (or development) of populations dominated by cautious foragers that specialize on fruits that can be processed in safe microsites.

Diversity of behavioural types within populations also matters. If different behavioural types differ in seed dispersal strategies and outcomes, then within-population variation in behavioural types (mechanism 2) can result in seeds being deposited in a more diverse array of places, including a greater range of distances away from parent plants. This will result in dispersal kernels with fatter tails, relative to a situation without behavioural types. However, this effect is not the only consequence of variation in behavioural types. For example, more cautious, less exploratory animals are likely to move seeds to more 'familiar' microhabitats near the parent plant, while more exploratory, bolder animals move seeds to new habitats far from parent plants. The increased microsite variability can then reduce variance in plant success via a *portfolio effect* (Bolnick et al., 2011). This leads to the notion that a single species consisting of individuals with different behavioural types might serve different roles in the community, analogous to multiple species (Sih et al., 2012). Furthermore, this might lead to a situation in which certain individuals play a particularly important role in seed dispersal and cannot be replaced by others (i.e. keystone seed dispersers).

Perhaps most interestingly, behavioural syndromes can result in correlations among outcomes of the multiple stages of the dispersal process (mechanism 3). For example, behavioural syndromes can generate conflicts or trade-offs in which a behavioural type that enhances seed dispersal success in one stage, reduces success in another (Figure 1). Bold, active individuals that have a fast metabolism (Réale et al., 2010) can be poor dispersers if they collect fewer seeds before moving on (weaker area-concentrated search: Spiegel, Leu, Bull, & Sih, 2017), and have a higher likelihood of consuming them (due to their higher energy demands). However, these bold individuals might offset lower dispersal rates by being more likely to



**FIGURE 1** Hypothetical trade-offs involved in seed dispersal by (a) proactive individuals (scoring high for boldness, aggression, activity and exploration) and (b) reactive individuals (scoring low for these traits), illustrated with an example of a scatterhoarding rodent. Red boxes denote animal decisions that are potentially detrimental to plant recruitment; green boxes denote advantageous ones. Size of the boxes reflects relative probability of a given decision (or relative contribution to plant recruitment) for proactive versus reactive animals. In comparison to reactive individuals, proactive individuals are more likely to harvest encountered seeds (especially when foraging is conducted under high predation risk) but also more likely to eat rather than cache them. Furthermore, proactive individuals are predicted to disperse seeds on average further than reactive individuals and hide them in open habitats (often advantageous for seedling recruitment, which is indicated with the seedling size) rather than in habitats with dense cover. Note that the predicted impact of proactive versus reactive types is highly context-dependent and the illustration denotes only one of several possibilities (see main text). Illustration credit: Emily Underwood

move seeds farther and to deposit them in open microsites with low competition for seedlings. Fast, proactive behavioural types (bold, aggressive, active, exploratory) have also been associated with a cognitive style that emphasizes speed over accuracy (Sih & Del Giudice, 2012). A plausible, but rarely tested hypothesis is that these proactive behavioural types (relative to reactive behavioural types) might exhibit less sampling behaviour and information collection, and less reliance on memory and spatial maps, all of which can be critical for outcomes of frugivory and scatterhoarding (John, Soldati, Burman, Wilkinson, & Pike, 2016).

Importantly, behavioural syndromes cause seed dispersal traits to correlate with other ecologically relevant behaviours for seed dispersal (e.g. such as predator avoidance and mating tactics). These relationships may produce carryover effects in which natural or sexual selection in other contexts affect seed dispersal. For example, it is well known that predation risk often has the immediate, direct effect of causing seed dispersers to hide more and move less, which affects their efficacy as seed dispersers (Breviglieri, Piccoli, Uieda, & Romero, 2013; Breviglieri & Romero, 2016; Sunyer, Muñoz, Bonal, & Espelta, 2013). Additionally, high risk can induce development or evolution of animals with more cautious behavioural types, who hide and are relatively inactive even when predators are not actually present. Along parallel lines, sexual selection can favour more aggressive or bold male behavioural types that then differ in both personality and dispersal traits from females. Colonization, invasion, range expansion and urbanization are often associated with bolder, more aggressive or more exploratory animals (Chapple, Simmonds,

& Wong, 2012; Cote, Fogarty, Brodin, Weinersmith, & Sih, 2011; Duckworth & Badyaev, 2007). We predict that these animals will differ in their efficacy as seed dispersers compared to 'resident' animals.

## 5 | EFFECTS OF BEHAVIOURAL TYPES AT DIFFERENT STAGES OF SEED DISPERSAL

### 5.1 | Encountering fruits

Fundamentally, the probability of encountering fruits depends on the movement patterns of foragers (Côtés & Uriarte, 2013); animal movements exhibit striking inter-individual variation, even after accounting for effects of species, age, size and sex. A substantial proportion of this variation appears to result from the linkage between movement and behavioural types (Spiegel et al., 2017).

Behavioural types influence home range size (Alós, Palmer, Rosselló, & Arlinghaus, 2016; Campioni, Delgado, & Penteriani, 2016; Schirmer, Hoffmann, Eccard, & Dammhahn, 2020; Villegas-Ríos, Réale, Freitas, Moland, & Olsen, 2018) and the use of space within it (Boon, Réale, & Boutin, 2008; Schirmer et al., 2020; Spiegel, Leu, Sih, Godfrey, & Bull, 2015; van Overveld & Matthysen, 2010). Home range size determines how many fruiting plants and plant species can be potentially encountered. The chances of finding particular fruits within the home range are affected by the exploratory activity of a given individual. Many



species of animals exhibit consistent, intraspecific differences in exploration, which can be placed along a continuum between fast and superficial versus thorough and slow (Réale et al., 2007). The fast and superficial explorers are more likely to be the first to find fruits that are more obvious, for example fruits that are larger, brighter or produced in higher quantities (Table 1). On the other hand, the slower and more thorough explorers can avoid competition by focusing on less obvious fruit. These differences could lead to specialization in dispersal of different fruit species (by 'specialization', we mean relative proportions in the diet, as vertebrate frugivores typically forage on many species of fruits and do not depend on a single plant for survival; Herrera, 2002).

The probability of fruit encounter is likely to be further modified by individual differences in boldness (Table 1). In social animals, bolder individuals are more often located at the edges of the groups and thus are more likely to collect personal information on food sources and act as 'producers', whereas shy animals usually forage closer to the centre of the group and are more likely to rely on information from others for foraging, thus acting as 'scroungers' (Flynn & Giraldeau, 2001; Kurvers et al., 2010). In other systems, scroungers aggressively appropriate resources (e.g. Lee & Cowlshaw, 2017) and in this case aggressive individuals would act as scroungers.

Moreover, foraging on temporally variable resources such as fruits requires tracking resource levels and remembering visited patches (Corlett, 2011; John et al., 2016). Thus, fruit-frugivore encounters can be affected by the link between behavioural types and cognitive differences (Sih & Del Giudice, 2012). For example, bold, proactive individuals often rely more on established routines, and therefore have higher site fidelity than shy, reactive individuals, which tend to build more thorough spatial maps of their home ranges and be more responsive to changes in the environment (Herborn, Heidinger, Alexander, & Arnold, 2014; Sih & Del Giudice, 2012).

Finally, in addition to affecting how animals forage, behavioural types influence where animals do it. Sensitivity to predation risk is a major mechanism that underlies this choice. Bolder individuals are more likely than shy ones to visit places that are more exposed or have indicators of predator presence, while shy animals preferentially forage in less open places (Sih, Bell, Johnson, & Ziemba, 2004; Toscano et al., 2016; Table 1) where they may encounter different quantities and types of fruit (Levey, 1988). Since boldness is also often associated with fast exploration and reliance on routines, whereas shyness is associated with slow exploration and flexible responses to environmental changes, behavioural types likely will affect fruit-frugivore encounters through complex links between foraging modes, responses to predation risk and habitat choices.

## 5.2 | Decision to harvest versus ignore

Standard optimal diet theory suggests that the influence of behavioural types on diet choice (harvest vs. ignore) should depend on how behavioural type affects encounter rates. An obvious prediction is that, all else equal, more exploratory and active foragers should

have higher encounter rates with potential food items and should thus be more likely to specialize on and disperse higher quality fruits (e.g. fruits that yield more energy per unit handling time) and reject lower quality ones (Table 1). In agreement with this reasoning, bolder deer mice *Peromyscus maniculatus* preferred heavier artificial seeds than more shy individuals (Brehm et al., 2019).

In addition, when food items are found in clusters, as is often the case with fruits on plants, then diet choice depends on patch choice. Patch choice, in turn, depends on patch quality (e.g. on fruit abundance on a focal tree) rather than the quality of individual fruits, on predation risk while foraging in the patch, and costs of travelling between patches. When travel costs are high (in terms of time, energy or predation risk), foragers should spend more time in higher-density fruit patches even if individual fruits in such patches are less preferred than fruit in lower-density patches. For example, Levey, Moermond, and Denslow (1984) demonstrated that even moderate spacing of preferred fruit caused birds to switch to a less preferred fruit (notwithstanding considerable between- and within-species variation). We predict that bolder, more highly exploratory individuals will give less weight to costs of travelling time when trading off the benefits and costs of foraging (Table 1).

Territorial frugivores might monopolize some fruiting plants, chasing away conspecific and heterospecific competitors (Howe, 1986; McConkey & Drake, 2006), often to the detriment of seed dispersal. In this situation, most seed dispersal will be provided by the territorial individuals. Similarly, dominance hierarchies in group-living frugivores might limit seed dispersal by low-ranking individuals. Yet, when fruits are non-preferred as food items, they will be dispersed mainly by subordinates (Tsuji, Campos-Arceiz, Prasad, Kitamura, & McConkey, 2020). The ability to monopolize food resource is often correlated with high aggression levels and proactive behavioural types (Briffa, Sneddon, & Wilson, 2015; Table 1).

When encountered fruits or seeds are novel, behavioural types will likely influence whether animals approach and try to ingest them. Bold and fast exploring individuals tend to be relatively neophilic, whereas shy, slow exploring ones are relatively neophobic (Exnerova Svádová, Fučíková, Drent, & Štys, 2010; Rockwell et al., 2012; Stuber et al., 2013). This suggests that when plants are rare (e.g. during the initial stages of biotic invasions), a subset of bold, proactive individuals can be disproportionately important as dispersers of their seeds.

Furthermore, the decision whether to forage and which fruits to ingest is under the obvious influence of the metabolic state and dietary needs of the forager (Corlett, 2011; Toscano et al., 2016). A large body of work links behavioural types with metabolism (reviews in Biro & Stamps, 2010; Careau, Thomas, Humphries, & Réale, 2008; Holtmann, Lagisz, & Nakagawa, 2017; Mathot et al., 2019). The recurring theme is that proactive individuals, characterized by high exploration rates, boldness and aggressiveness, need more energy to sustain their activity levels (Careau et al., 2008; Stamps, 2007, but see Careau et al., 2015; Krams et al., 2017 for examples of more complex relationships between behavioural types and metabolic rates). If proactive animals have a higher food intake, they could disperse a higher quantity of seeds from a greater diversity of plant species (Table 1; Figure 1).

Pioneering data on forest rodents support these concepts. In red-backed voles, boldness positively affected removal rates of novel (artificial) seeds (Brehm et al., 2019). In deer mice, activity scores were positively correlated with the probability of removing experimental seeds and the probability that removed seeds will be consumed (Brehm et al., 2019).

### 5.3 | Dispersal distance

With the exception of relatively rare events such as natal dispersal or migration, home range size sets an upper limit on seed dispersal distances (Fuzessy, Janson, & Silveira, 2017). Thus, factors that control home range size and exploration patterns of frugivores (see Section 5.1) will affect average distances they disperse seeds, with proactive individuals generally expected to disperse seeds further than reactive ones (Table 1; Figure 1). However, this relationship is likely to be clearer in solitary rather than group-living animals (because ranging patterns of proactive and reactive individuals will be similar when they move in the same group) and can be modified by additional factors. For example, in frugivorous fish, gut passage time is increased by physical activity (Van Leeuwen, Beukeboom, Nolet, Bakker, & Pollux, 2016), which can inflate seed dispersal distance by highly exploratory individuals (acting synergistically with the effect of greater distances travelled by such animals). In birds, gut passage time is affected by diet (Karasov & Levey, 1990; Traveset et al., 2007); thus, individual differences in diet might provide another factor influencing distances of seed dispersal provided by animals with different behavioural types. This mechanism is probably less important in mammals (Campos-Arceiz et al., 2008).

Seed dispersal distance can also be modified by boldness of the dispersers (Table 1). When animals forage on patchy food resources, boldness affects when animals cease feeding and move to another patch (Mella, Ward, Banks, & McArthur, 2015). This threshold (aka 'giving-up density': Brown & Kotler, 2004) is determined by the interplay between benefits of foraging, which decrease as the forager gets satiated or the patch gets depleted, and the perception of predation risk. For frugivores, foraging patches are often represented by different trees. If trees are safe sites, shy (cautious) animals will be less willing to leave patches, while bold ones will be more willing to move on and thus disperse seeds. If trees with fruit are not safe sites, then bold individuals that forage longer before the perceived risk outweighs the benefits have higher chances of depositing seeds under the parent tree. Shy animals, on the other hand, are more likely to 'give-up' and leave an unsafe fruiting tree quickly (Table 1). If they leave to retreat to safety, then how far they go will depend on the distance to refuge; that is, the spatial distribution of foraging patches and refuges could be critical for determining dispersal distances for shy animals. This effect is most likely to occur in species with short gut passage times, such as many birds (Levey & del Rio, 2001). A similar boldness-based mechanism might occur in animals that decide whether to eat on the spot or carry fallen fruits

or seeds into safer places for consumption (Lima & Valone, 1986), with the latter potentially resulting in longer-dispersal distances (Table 1), depending again on the spatial distribution of foraging sites and refuges.

First empirical results support the notion on the link between boldness and dispersal distance. In a study on red-backed voles *Myodes gapperi*, bolder individuals dispersed artificial seeds further than shy ones (Brehm et al., 2019). There might also be connection between anxiety and seed dispersal distance. Captive wood mice *Apodemus sylvaticus* that displayed more 'stressed' behaviour in their home terraria, dispersed acorns further than animals that displayed more 'relaxed' behaviour (Feldman et al., 2019). It is noteworthy that these patterns remained unaffected by predator scent treatment, perhaps because rodents are more sensitive to indirect predation cues (such as microhabitat structure; Orrock, Danielson, & Brinkerhoff, 2004). However, in free-living deer mice that dispersed artificial seeds, the relationship between anxiety and dispersal distance was reversed: low anxiety individuals dispersed artificial seeds further than high anxiety individuals (Brehm et al., 2019).

Effects of individual differences in aggressiveness on seed dispersal distance will depend on the role of agonistic social interactions in determining movement and space use. For example, in many frugivorous bats, some individuals forage at fruiting trees (dropping seeds directly below) and actively defend trees from intruders, while others attempt to snatch the fruits and carry them away for consumption (McConkey & Drake, 2006; Richards, 1990). In this case, aggressive individuals are less likely to disperse seeds away from mother trees (Table 1). See also McConkey and Brockelman (2011) for similar effect of aggressive interactions on seed dispersal in group-living macaques.

### 5.4 | Seed condition after fruit processing

Seeds dispersed by frugivores often benefit from pulp removal and seed coat abrasion during handling or gut passage, but seeds can also be damaged in the process. Thus, the condition of deposited seeds can be influenced by the link between behavioural types, mobility and gut passage time (which is typically shorter in highly active individuals). Sometimes, increased physical activity contributes to higher viability of seeds after gut passage (Kleyheeg, Van Leeuwen, Morison, Nolet, & Soons, 2015). However, the most common relationship between gut passage time and seed viability is likely to be unimodal because too short gut passage might not break seed dormancy, but too long might kill the seed (Jaganathan et al., 2016; Traveset et al., 2007; Table 1). If this is the case, seeds dispersed by animals with intermediate activity, and thus intermediate gut passage times, will have the highest viability.

Perhaps less intuitively, seed condition might also be affected by the dominance rank of foragers. Behavioural types influence the ability to win contests (Briffa et al., 2015), which in turn might determine how seeds are processed (e.g. chewed faster and less thoroughly by subordinate individuals due to risk of harassment by



dominants). For example, in macaques, high-ranking individuals were more likely than low-ranking ones to damage seeds during mastication (Tsuji et al., 2020). Still, this idea would benefit from further testing because current evidence is rather limited.

## 5.5 | Deposition site

Directed dispersal to sites where seed survival is particularly high is one of the most important services provided by frugivorous and granivorous animals (Hirsch, Kays, Pereira, & Jansen, 2012; Salazar et al., 2013; Wenny, 2001; Yi, Liu, Steele, Shen, & Liu, 2013). While most existing studies of directed dispersal tend to focus on interspecific differences among dispersers in seed deposition sites, some indicate that intraspecific differences are equally relevant in determining where seeds are dispersed (Jadeja, Prasad, Quader, & Isvaran, 2013; Wenny & Levey, 1998). However, the role of behavioural types in providing dispersal into non-random sites (either particularly favourable or particularly unsuitable for plant recruitment) remains overlooked. As an exception, Brehm et al. (2019) reported that scores in a handling bag tests were associated with cache locations in red-backed voles. Individuals that tended to remain immobile rather than struggle during handling preferred coarse woody debris for caching seeds, while less docile voles preferred tree bases.

Deposition sites are linked to foraging patterns but are also influenced by non-foraging behaviours, such as resting, courting or patrolling territories (Sasal & Morales, 2013; Wenny & Levey, 1998). Thus, deposition sites are affected by habitat choices of seed dispersers (Da Silveira, Niebuhr, de Lara Muyaert, Ribeiro, & Pizo, 2016; Herrera, de Sá Teixeira, Rodríguez-Pérez, & Mira, 2016; Rodríguez-Pérez, Wiegand, & Santamaria, 2012), which in turn strongly depend on individual boldness, as described above (sections 5.1 and 5.2). In environments where plants compete for light (e.g. most forests), rare, ephemeral open areas often represent a hotspot of plant recruitment (Brodie et al., 2009; Leemans, 1991; Rüger, Huth, Hubbell, & Condit, 2009; Schupp, Howe, Augspurger, & Levey, 1989; Svoboda et al., 2012). Thus, bold individuals are likely to be crucial for seed dispersal into recently created forest gaps, which are perceived as risky by most frugivorous animals, but provide excellent conditions for recruitment of many species of plants. On the other hand, in hot, dry environments, deposition under nurse plants is more favourable than in the open (Derroire, Tigabu, Odén, & Healey, 2016; Muñoz & Bonal, 2007; Vander Wall, 1997). Thus, the role of bold and shy individuals in providing directed dispersal should change with environmental context (Table 1).

Sociability (Réale et al., 2007) of individual seed dispersers and consistency (Biro & Adriaenssens, 2013) of their movement patterns can affect patterns of seed aggregation, with seeds deposited in higher densities by individuals that are highly social or by individuals that consistently visit the same sites (Table 1). Such clumped seed deposition is likely to result in strong, negative

density-dependent effects on survival, germination and growth (e.g. Russo & Augspurger, 2004).

Finally, seed deposition in dung can be thought as a form of direct dispersal because faeces can have a positive, fertilizing effect of seedlings (Sugiyama et al., 2018). The magnitude of this effect can vary among individuals; depending on their diet, dung can differ in nutritional composition and water-holding capacity (Traveset et al., 2007). Such differences are particularly evident in carnivores and omnivores, where fruits are just a fraction of a varied diet (Traveset et al., 2007). However, the link between behavioural types and diet choice is particularly understudied.

## 6 | THE SPECIAL CASE OF SCATTERHOARDING GRANIVORES

### 6.1 | Partial seed consumption

The decision to give up foraging before the seed is completely eaten is likely to be affected by risk perception in a manner analogous to giving-up density (Brown & Kotler, 2004). Thus, compared to shy individuals, bold ones are predicted to consume a higher proportion of the cotyledon (damaging each seed more) or to eat entire seeds, hence acting as predators rather than dispersers (Table 1).

Partial versus complete seed consumption is also likely affected by the metabolic state of the forager. The pace of life hypothesis predicts that proactive, bold animals require more energy (Réale et al., 2010), and are thus less likely to discard seeds that are only partially eaten (Table 1). Due to the link between boldness and metabolic rates, the risk-driven and the energy-driven mechanisms are expected to co-occur and reinforce the outcome: proactive individuals should eat entire seeds or larger proportions of individual seeds than reactive ones, thus having a more negative effect on plant recruitment than reactive individuals.

### 6.2 | Decision to eat versus cache seeds and the fate of cached seeds

Scatterhoarding is thought to have evolved as a strategy of food caching used by animals that are unable to actively defend stored food from thieves (Vander Wall, 1990). In line with this notion, individuals of some granivore species engage in either scatterhoarding or larderhoarding, depending on individual capabilities of larder defence (Clarke & Kramer, 1994). Thus, besides obvious factors such as body size and strength, the probability of scatterhoarding versus larderhoarding will likely be affected by the caching animal's aggressiveness (Table 1). Individuals that are highly aggressive and defend larders would negatively affect plant recruitment, whereas less aggressive, scatterhoarding individuals would more likely act as mutualistic seed dispersers.

Given that the strategy of preserving food for future use is beneficial only when hoarders survive long enough to use their caches

(Andersson & Krebs, 1978), proactive, bold individuals, which invest in current rather than in future reproduction (Biro & Stamps, 2008; Réale et al., 2010; Wolf et al., 2007), are less likely to cache than are reactive individuals (Table 1). Furthermore, caching is more likely to occur when cache owners have a cache recovery advantage over potential pilferers (Andersson & Krebs, 1978; Smulders, 1998; R. Zwolak, D. Clement, A. Sih & S. Schreiber, in prep.). Some of this advantage can be a simple consequence of distribution of home ranges (as long as they do not overlap completely) but it also depends on the ability of scatterhoarders to remember cache sites (Gu, Zhao, & Zhang, 2017; Vander Wall, 2000; Wang, Zhang, Wang, & Yi, 2018). Pilferers, on the other hand, observe caching animals (documented mostly in corvids: Shaw & Clayton, 2014) or detect caches by searching at random or in response to scent cues (documented mostly in rodents: Dally, Clayton, & Emery, 2006). A recent study on Siberian chipmunks *Tamias sibiricus* suggested that ability to remember one's own caches versus detect caches made by other animals trades off among individuals (Yi, Wang, Zhang, & Zhang, 2016). While the link between behavioural types and specialization to cache versus pilfer seeds has not been investigated, reactive, slow-exploring animals are hypothesized to invest more into spatial memory than proactive, fast-exploring animals (Sih & Del Giudice, 2012). If such a relationship occurs, we predict that reactive individuals will specialize in scatterhoarding (because it involves memorizing cache locations; Wang et al., 2018; Yi et al., 2016), while proactive individuals will specialize in seed pilferage (because it requires intense exploration). Thus, several different lines of reasoning lead to the prediction that reactive animals will scatterhoard more intensely than proactive ones (Figure 1).

We note, however, that the success of fast and superficial versus slow and thorough exploration as pilferage strategies is likely to be context-dependent, varying with detectability of seeds. This trait depends on seed species (Cao et al., 2018), on soil moisture, which enhances seed odours (Vander Wall, 1998; Yi et al., 2013), and on substrate type (Briggs & Vander Wall, 2004). When cached seeds are relatively easy to locate, fast explorers are expected to pilfer more seeds, but when they are difficult to detect, slow explorers might fare better (Table 1).

Given the ubiquity of cache pilferage (Jansen et al., 2012; Vander Wall & Jenkins, 2003), it is not surprising that caching animals evolved strategies to reduce cache pilferage (reviewed in Dally et al., 2006). These strategies include caching in risky (usually open) habitats, where potential pilferers are less likely to venture (Muñoz & Bonal, 2011; Steele et al., 2014). This approach involves a trade-off between the risk of losing caches to pilferers and the risk of being predated while transporting and handling seeds. Clearly, it should be used more readily by bold than by shy individuals (Figure 1). At the same time, the strategy of caching in risky places should be most successful against relatively shy pilferers (Table 1). Thus, the success of particular behavioural types and their associated strategies is likely frequency-dependent, resulting in a game aspect in the interactions between bold and shy scatterhoarders.

## 7 | CONSEQUENCES OF VARIATION IN EFFECTIVENESS AT DIFFERENT STAGES OF SEED DISPERSAL

We divided seed dispersal into separate stages and used these steps as a structure for organizing our ideas. Successful seed dispersal, however, typically requires favourable outcomes at multiple stages (Schupp et al., 2010; Figure 1). The fact that personality can affect multiple stages of the seed dispersal process has interesting implications for plant fitness, particularly when there are trade-offs where a given behavioural type increases dispersal success in one step, but reduces it in another. Since overall success is the multiplicative product of these steps, it involves the geometric (not arithmetic) mean of success in these stages. This favours lower variance in success in each stage (i.e. bet hedging). Thus, all else the same, behavioural types that provide moderately efficient dispersal at each stage should be better for plants than behavioural types that are very efficient on some steps, but ineffective on others.

In addition, as emphasized by life-history theory and projection matrix analyses (e.g. Caswell, 2000), the increase in plant fitness associated with the same proportional increase in dispersal success can differ across stages of dispersal depending on the *elasticity* of survival in that stage. In life histories with very low survival to establishment, early stage individuals (hatchlings, newly released seeds) often have very low reproductive value such that an increase in their survival can have relatively little effect on overall population success (recall the classic example with marine turtle hatchlings; Crouse, Crowder, & Caswell, 1987). In contrast, individuals that have 'made it' almost to establishment have higher reproductive value so a proportionally similar increase in their survival has a much larger benefit for population success. Following this logic, behavioural types that are more effective than others at depositing seeds in high-quality sites can be more beneficial for plants than ones that are simply effective at moving seeds away from parent plants. More generally, behavioural types that enhance seed success in high elasticity stages should have particularly large beneficial impacts on plant fitness, even if they have minor detrimental effects on success in low elasticity stages.

## 8 | BEHAVIOURAL TYPES AND ANTHROPOGENIC INFLUENCES ON SEED DISPERSAL

Seed dispersal is strongly affected by human activity, including hunting, logging, fragmentation, and more subtle but equally widespread effects such as pollution with anthropogenic noise or light (Francis, Kleist, Ortega, & Cruz, 2012; Markl et al., 2012; McConkey et al., 2012). Animal personalities are likely to mediate some of these shifts in seed movements. Human-induced environmental changes select for particular behavioural types (and consequently seed dispersal characteristics) through mechanisms that include microevolution and personality-dependent habitat choice (Lapiedra,

Chejanovski, & Kolbe, 2017; Miranda, Schielzeth, Sonntag, & Partecke, 2013). In many cases, humans create conditions that are either more dangerous for seed dispersing animals or perceived by them as more risky. For example, fragmentation often negatively affects seed dispersal because (a) animals may decide not to cross open spaces between habitat fragments (Herrera et al., 2016); (b) anthropogenic noise makes it more difficult to detect approaching predators and therefore affects the foraging-vigilance trade-off (Barber, Crooks, & Fristrup, 2010) or (c) human presence is perceived as dangerous and areas visited by humans might be avoided by seed dispersers (Bötsch, Tablado, & Jenni, 2017; Haigh, Butler, O'Riordan, & Palme, 2017; Ranaweera, Ranjeewa, & Sugimoto, 2015). In all such cases, boldness is likely to be a crucial personality trait, with bold, risk-tolerant individuals providing seed dispersal services in situations where more shy individuals cease to do so (see Brehm et al., 2019 for a forest logging example).

However, in addition to affecting risk perception, boldness can also influence susceptibility of individual seed dispersers to human-related mortality. There has been substantial concern about the effects of poaching and hunting on animal-mediated seed dispersal (Harrison et al., 2013; Peres, Emilio, Schietti, Desmoulière, & Levi, 2016; Terborgh et al., 2008). Understandably, the main focus has been on rapid declines in the abundance of key dispersers. However, hunting will likely also have more subtle effects, above and beyond direct effects on population abundance (e.g. McConkey & Drake, 2006). Humans often selectively remove bolder and more active individuals from the harvested populations (Biro & Post, 2008; Biro & Sampson, 2015; Diaz Pauli & Sih, 2017; Klefoth, Skov, Kuparinen, & Arlinghaus, 2017; Stuber et al., 2013). Thus, even when the hunted species is still present, the individuals that provide important seed dispersal services in disturbed landscapes might already be missing. In such a situation, negative effects of hunting on seed dispersal would be stronger than predicted solely by its effects on species abundance (see a review by McConkey & O'Farrill, 2016 for more details). Moreover, different human-induced environmental changes typically co-occur and magnify their ecological effects. For example, fragmentation often goes hand-in-hand with increased hunting pressure (Markl et al., 2012; McConkey et al., 2012), and bold individuals that provide keystone seed dispersal services in fragmented landscapes are usually disproportionately affected by hunting (cf. Côté et al., 2014), exacerbating the effects of fragmentation.

## 9 | CONCLUSIONS

We have outlined diverse mechanisms that potentially link behavioural tendencies with seed dispersal outcomes and have used behavioural types as a hypothesis-generating framework to make novel predictions on animal-mediated seed dispersal (summarized in Table 1). These predictions are based mostly on theoretical expectations because empirical research on this phenomenon is in its infancy. Thus, they represent ideas that need to be tested with future experiments or observations. We strongly encourage such

studies; benefits include not only a more complete understanding of ecological consequences of behavioural syndromes (Sih et al., 2012; Toscano et al., 2016; Wolf & Weissing, 2012) but also a more mechanistic understanding of animal-mediated seed dispersal and plant regeneration (Zwolak, 2018). Based on results of a recent meta-analysis (Des Roches et al., 2018), we anticipate that in many cases the effects of behavioural tendencies on animal-mediated seed dispersal will be comparable in magnitude to the effects of interspecific differences in disperser behaviour. An important challenge, however, will be to understand the generality of particular effects, as the strength and exact form of the associations between behavioural types and cognitive, physiological and life-history traits (which form the foundation of our framework) appear to exhibit considerable interspecific variation (Dougherty & Guillette, 2018; Niemelä & Dingemanse, 2018).

The time to conduct such studies is now. The rise in interest in ecological consequences of individual variation has coincided with the emergence of new technologies that allow researchers to monitor activity and movement of individual animals (e.g. Nathan & Giuggioli, 2013). Equally important is our ability to monitor the movement and fate of individual seeds through such techniques as radiotelemetry (Hirsch, Kays, & Jansen, 2012) or passive integrated transformer (PIT) tags (Suselbeek, Jansen, Prins, & Steele, 2013). In addition, seeds or seedlings can be tracked back to their mother plants with genetic analyses, thus enabling examination of direct consequences of animal-mediated seed dispersal (Ashley, 2010; Broquet & Petit, 2009; Godoy & Jordano, 2001; Grivet, Smouse, & Sork, 2005). Although the genetic methods to do so have been available for a while, they are becoming increasingly accurate, inexpensive and accessible. They have been used to identify species responsible for dispersing individual seeds (González-Varo, Arroyo, & Jordano, 2014) and in principle could be used also to identify individuals responsible for dispersal of those seeds. Furthermore, we possess newly developed statistical procedures that can link behavioural types to their ecological effects without inflating type I error (Houslay & Wilson, 2017). However, this improved rigor comes at the price of increased complexity of analyses and, most critically, considerably higher sample size requirements. While in some cases the recommended sample size can be difficult to reach, conducting fewer, but higher-powered studies might ultimately result in more reliable knowledge (Benjamin et al., 2018; Forstmeier, Wagenmakers, & Parker, 2017). Finally, empirical case studies should be complemented and broadened by mathematical models to further refine the theory of behavioural types and animal-mediated seed dispersal and guide its subsequent tests in the field. We look forward to future developments in this exciting research area.

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## AUTHORS' CONTRIBUTIONS

R.Z. and A.S. conceived the ideas and wrote the manuscript.

## DATA AVAILABILITY STATEMENT

There are no data to archive.

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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