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ABSTRACT

We studied four aspects of the dispersal of bramble by badgers: plant distribution, occurrence of fruits in diet, lack of damage to seed during ingestion, and beneficial effects on seed germination. The distribution of bramble plants was concentrated around a main sett and associated latrines. Examination of fresh badger dung samples in October 1992 showed that plants represented the main food items, with bramble seeds being by far the most common seeds present. Scanning electron microscopy of seeds before and after passage through the gut of badgers revealed little damage but for a reduced extent of the surface reticulations. Egested seeds exhibited a faster rate of germination than seeds in intact fruits or those washed clear of pericarp tissue. These results suggest that badgers are effective dispersers of brambles in Ireland.

INTRODUCTION

Seed dispersal is a central issue in ecology (Janzen 1982; Clobert *et al*. 2012). Dispersal of fruit-bearing plant species by carnivores has been reported since the 1930s (Ridley 1930). More recently, Herrrera (1989) and Traba *et al*. (2006), for example, presented evidence of seed dispersal by red fox *Vulpes vulpes* (L.), martens *Martes* sp. as well as by badgers *Meles meles* L., while dispersal of seeds by North American carnivores was reviewed by Willson (1993). She pointed out that their short digestion time, coupled with their large size and high mobility makes carnivores good dispersal agents for fruit. The germination of seeds after passing thorough the digestive tracts is an important aspect of such dispersal by carnivores (Traveset 1998; Fedriari & Delibes 2009; López-Bao & González-Varo 2011).

Badgers are the subject of considerable research in Ireland (Byrne *et al.* 2012). It is common to find brambles, *Rubus fruticosus* L. agg., at badgers' setts (e.g. O'Corry-Crowe *et al.* 1993, and it has been reported that badgers consume significant amounts of fruit in Ireland (Boyle & Whelan 1990; Cleary *et al.* 2009) and elsewhere (Kruuk & De Koch 1981; Roper & Mickevicius 1995; Mysłajek *et al*. 2013). During studies around badger sites as part of a research programme on the role of badgers in the spread of bovine tuberculosis (*Mycobacterium bovis*, BTB), it was observed that high densities of brambles were detected close to setts and latrine sites.

Here we investigate the effectiveness of the dispersal of brambles by badgers, study the condition of seeds consumed by badgers, and the resultant effects on germination of egested bramble seeds, and the distribution of bramble plants relative to badger setts and latrine sites.

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METHODS

Study Areas

The first study area was pasture and woodland at Warrenscourt, County Cork, Ireland. BTB was present in badgers in this area (Sleeman & Mulcahy 2005), and it became necessary for us to avoid exposure to the disease. The second site was Fota Estate which is in Cork Harbour, Ireland. It was a lowland estate, of 316 ha of mixed woods and parkland, of which approximately 50 ha were wooded; the Fota badger population was free of BTB (Southey *et al.* 2001). Blackberries were collected in both areas in October 1992.

Data collection

The distribution of bramble plants at a badger's sett and at latrines was mapped at Warrenscourt (Figure 1). The Warrenscourt Estate had active badger research on-going during the research period including bait-marking of latrines and focused on one main sett and one badger social group (Figure 1).

Forty fresh faeces were collected at badger latrine sites at Warrenscourt over a 23-day period from 9th October to 31st October (Figure 2). All samples were autoclaved in aluminium trays, to ensure destruction of any bacteria. Each dropping was passed through a porcelain filter (pore size 0.70 mm) and washed. The components from prey items retained by the filter were identified at 10x magnification. Seeds were identified by use of a reference collection, and the number of seeds of each species was recorded (Tables 1 and 2). Seeds were examined for damage. The diet items were identified using standard keys, for example, birds and mammals using feathers or hairs, in the latter case guard hairs. The percentage frequency of the different prey items was determined. The egested bramble seeds were collected for germination studies from fresh badger droppings at Fota in October.

The surface of seeds isolated from fresh bramble seeds, or from badger droppings, were compared at 180x magnification, using a 20kV, Jeol JSM scanning electron microscope following sputter coating of the samples with gold. To determine whether effects on seeds of passage through a badger gut were due to the acid conditions of the stomach contents, the pH of five dead badgers killed on the road was determined using a pH electrode and meter.

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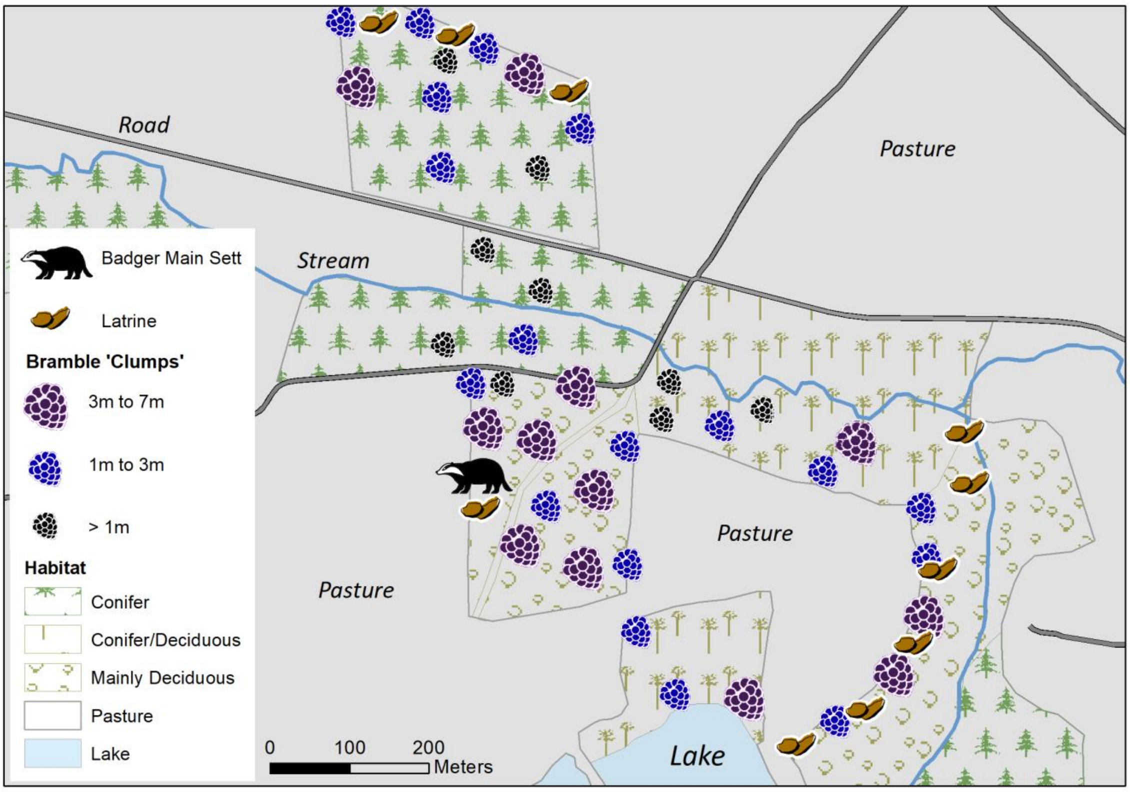

Figure 1. A simplified diagram of the badgers' main sett (burrow) and latrines where seeds were collected around Warrenscourt, with general habitat features.

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Three bramble seed treatments were investigated: (a) seeds in intact fruits, (b) seeds manually extracted from intact ripe fruits and wiped clean of attached pericarp tissue, and (c) seeds extracted from fresh badger dung. Ripe bramble fruits were selected on the basis of a uniform black colour, without red or purple coloration, from the sett and latrine sites in the study area and were used as the source of the seeds in treatments (a) and (b). Four 50-seed replicates from each treatment were set up in a glasshouse (minimum temperature 16 °C). The actual number of seeds in treatment (a) was determined from average seed counts per fruit and a subsequent count of non-germinated seeds after the experiment. A second trial was set up out-of-doors in early November and scored in spring to test the effect of low-temperature stratification on seed germination. In each case, the seeds/fruits were buried 1 cm deep in a pH 4.8 1:1 mix of loam soil and moss peat.

Item	Percentage frequency
Seeds	72.5
Grass fragments	62.5
Tipulid (Diptera) larvae	37.5
Beetles	35.0
Tree bark	32.0
Frog remains	2.5
Rabbit remains	2.5
Bird remains	2.5

Table 1. Relative frequency of food items found in samples of badgers' dung in October (n=40).

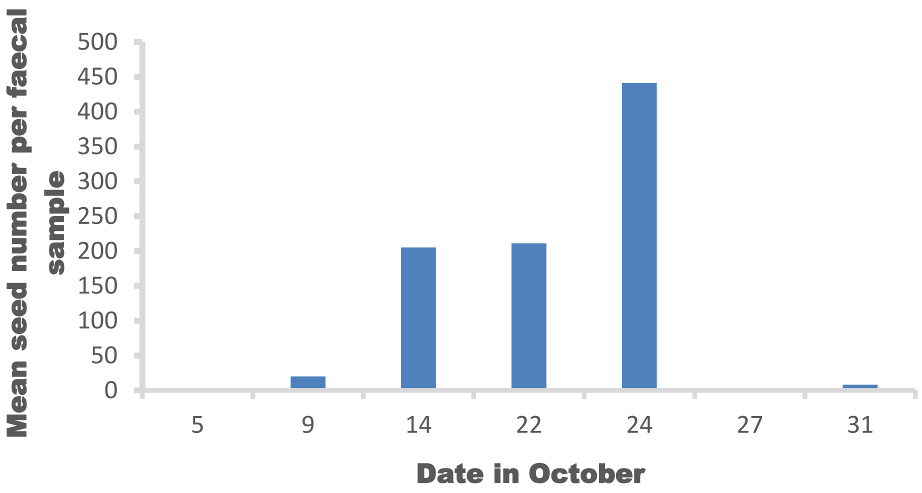

Figure 2. Temporal variation in number of bramble seeds in each badger faecal sample in October 1992.

RESULTS

Distribution of bramble stands around one main sett and associated latrines in Warrenscourt showed that clumps were associated with badger activities (Figure 1). Forty fresh dung samples were collected from latrines at Warrenscourt in October. Seven food types were identified, with seeds being the dominant type (Table 1); mammals, birds and frogs were rare (2.5%). Seeds were of twelve different plant species with bramble being the most frequent (Table 2). Bramble seeds were identified in 63% of the samples, while 86% (25 of 28) of the seed-containing samples contained bramble seeds. The only other plants whose seeds occurred frequently were elder (*Sambucus nigra*) and club-rushes (*Scirpus* sp.) (Table 2). Some dung samples had seeds of up to four plant species, but the most common situation was seeds of one species per dung sample.

Temporal variation was clear from the frequency of bramble seeds in dung samples, with more than 200 seeds per sample being recorded between 14th and 23rd October, but with fewer than 20 seeds per sample at earlier or later dates (Figure 2).

Microscopic examination of seeds extracted from fresh ripe fruits (on average, 30-50 seeds per fruit) revealed a reticulate structure to the testa, composed of ridges, which represented outgrowths of the integument of the ovule (Figure 3A). This compares with smoothed, less ridged surface of seeds that have passed through a badger (Figure 3B).

Seeds of brambles (n = 4710) recovered from dung exhibited little damage; the testa was damaged or the seed fragmented in 0.2% of the specimens. Seeds recovered from fresh dung collected from latrines exhibited a less sharply defined reticulate surface than manually extracted seeds, with the ridges and other structures being less pronounced (Figures 3A and B). The mean pH of the stomach of dead badgers was 6.03

(SD = 0.20, n = 5).

Seeds extracted from dung germinated first (week 17) in the greenhouse study, followed by those extracted from fresh fruits (week 18) and finally seeds from intact bramble seeds (week 20) (Figure 4). By early March (weeks 19 and 20), the percentage germination from each of the treatments differed significantly (χ^2 = 147.7, DF = 2, p<0.001), having reached 53% (seeds from dung), 18% (manually extracted seeds) and 2% (intact fruit), while germination at weeks 25 and 26 in each of the three treatments had plateaued, at 74%, 46% and 34%, respectively (χ^2 = 74.2, DF = 2, p<0.001). Results were broadly similar from the germination trial set up under outdoor conditions (data not shown).

Species		Percentage frequency
Bramble	*Rubus fruticosus* agg	86.2
Elder	*Sambucus nigra*	10.3
Sedges	*Scirpus* spp	10.3
Cleavers	*Galium aparine*	6.9
Barley	*Hordeum vulgaris*	6.9
Grasses	Poaceae	6.9
Raspberry	*Rubus idaeus*	3.5
Campion	*Silene spp*	3.5
Oat	*Avena sativa*	3.5
Enchanter's nightshade	*Circaea butetiana*	3.5
Stonecrop	*Sedum acre*	3.5

Table 2. Relative frequency of species whose seed were found in badgers' dung containing seeds (n= 29).

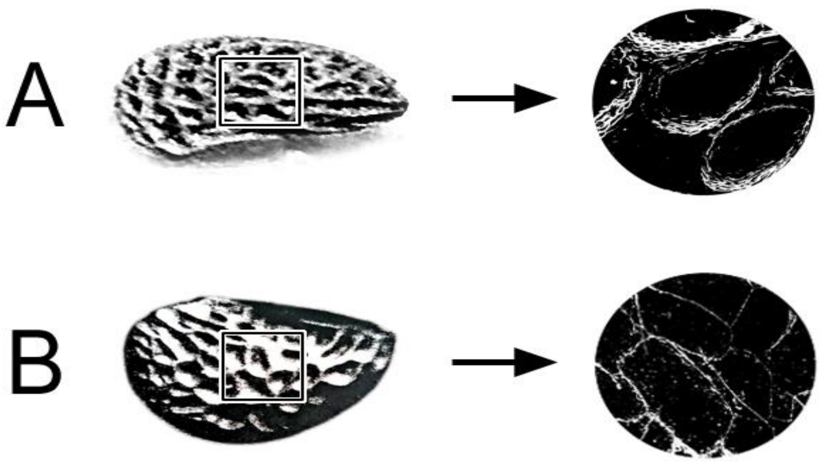

Figure 3. Representative specimens of bramble seeds manually extracted from ripe fruit (A) or extracted from badger dung (B). The image in the square is 180 × magnification. Note the more sharply defined surface structure of ridges and craters in A compared to B. These are different seeds.

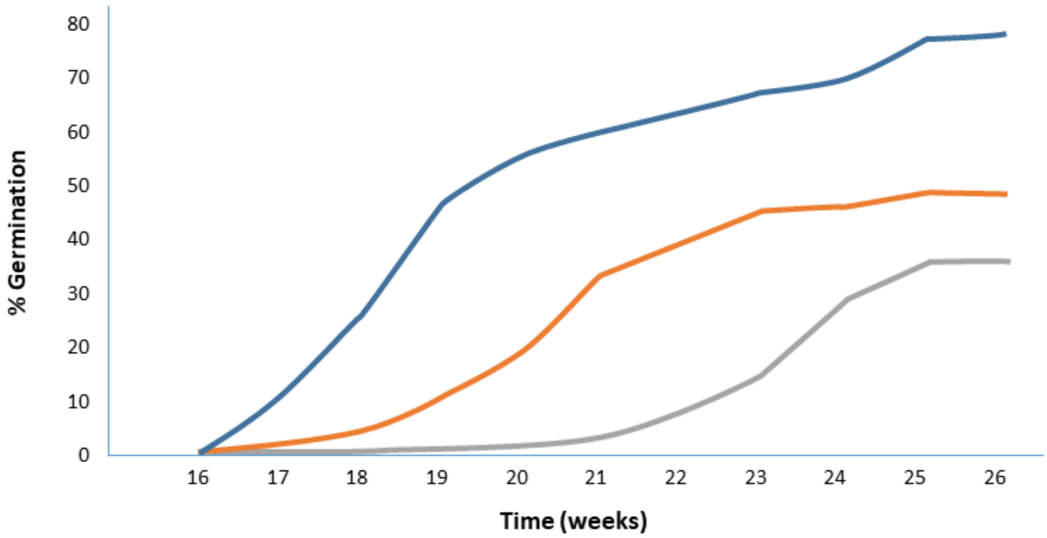

Figure 4. Effect of seed treatment on bramble seed germination. Seed treatments were seeds in intact fruits (grey), seeds extracted from fresh fruit (orange) and seeds collected from badger dung (blue).

DISCUSSION

Mutualistic interactions involving seed dispersal between animals and plants are at their most obvious in the tropics where reduced seasonality of fruit production makes obligate frugivory possible. A frequently mentioned example is of African acacia (*Acacia erioloba* Meyer) seeds which pass through the gut of African elephants (*Loxodanta africana africana* Blumenbach), and then germinate (Douglas-Hamilton & Douglas-Hamilton 1975; Kay 1992). Such interactions are often less obvious in temperate zones; however, they exist, for example, in Japan (Koike *et al.* 2008) and Spain (López-Bao & González-Varo, 2011), and should occur in the less complex ecosystems, such as those of the Balearic Islands (Clevenger 1996) or Ireland. It has been suggested that straight-tusked elephants *Elephas antiquus* caused damage which led to re-sprouting – or coppice - from snapped trunks in Europe before they went extinct, as African elephants do today, thereby improving the environment for themselves (Monbiot 2013). We suggest something similar for badgers.

Carnivores represent an under-recognised route for seed dispersal, in terms of dispersal distance and in the probability of seeds reaching new habitats. The results of our studies show that badgers consume bramble fruits in significant quantities in season and disseminate the seeds into suitable receiving habitats (e.g. latrines) in a largely undamaged condition from which germination rate is faster and higher than from seeds in intact fruits, all of which are criteria for an effective seed dispersal agent (Janzen 1981). Badgers in Ireland move 1-2 km each night, but can cover several home ranges, travelling distances of 7 to 22 km (Byrne *et al*. 2014). These are unusually long for badgers elsewhere in Europe.

The maximum frequency of bramble seeds was 450 seeds per dung sample collected on 24th October, which represents ten to fifteen bramble fruits (but still short of the 70% of the ingested food volume reported by Kruuk & de Koch 1981). The mean bramble seed content of dung samples over the entire period was 118 (SD = 40), equivalent to between 2.5 and 3.8 fruits. In most cases, brambles were the only seed present in dung samples (Table 2), suggesting that the badgers were targeting these fruits particularly, rather than fruits in general, despite the fact that elderberries (from *S. nigra*) were more common than bramble fruits in the study areas at the time of the study (data not shown).

Bramble seeds exhibit several traits characteristic of seeds dispersed by passage through the gut of a mammal, namely small size (2–3 mm), and ovoid shape with a reticulate and durable coat (Debussche & Isenmann 1989). This adaptation is reflected in the very low level of visible damage suffered by freshly excreted bramble seeds in the current study.

Not only did seeds pass through the badger digestive tract seemingly intact, but the passage appeared to stimulate germination, with excreted seeds germinating more rapidly and in greater numbers by mid- March than did those intact fruits placed one centimetre deep on the soil surface. Multiple mechanisms of dormancy are known to operate in rosaceous seeds, although seeds overwintered outdoors did not show any improved germination over those over-wintered at a constant 16 ^{o}C (MO'S: unpublished results), suggesting that dormancy was relieved by the removal of water-soluble germination inhibitors relieving physiological dormancy rather than by a low-temperature stratification effect.

Passage through the badger gut had several effects on the seeds. The fleshy outer pericarp of the fruit had been removed and the seeds showed evidence of scarification, as indicated by erosion of the testa ridges (Figure 3).

Manual removal of the pericarp was associated with accelerated germination, suggesting that the fruit contained germination inhibitors, but the germination rate of the washed seeds was still slower than that of excreted seeds. Scarification of seeds during digestion could increase permeability of the seed coat to water and gases and encourage embryo expansion. The highly acidic stomach environment of mammals is known to erode seed coats and affect germination of some plant species but measurements of the pH of the stomach contents of five dead badgers gave a surprisingly high mean value of 6.03. However, gastric pH determination can be affected by how long the badger had been dead and whether food was present in the stomach.

Rosalino *et al*. (2004) suggested that the spatial distribution of some carnivores was affected by occurrence of fruit-rich patches. We are suggesting that a carnivore, the badger, influences the distribution of bramble patches, by depositing seeds, which have been stimulated to germinate by passage through the gut, in appropriate nutrient-rich locations (latrines and around main sett entrances). This, in turn, will make the area better for badgers in the long run, with a local increase in food sources in the form of bramble patches (see also Obidzinski & Glogowski 2005). Pigozzi (1992) and Rosalino *et al*. (2010) also reported that passage through badgers promoted fruit seed germination.

Overall, our data indicated that, these animals target ripe bramble fruit as a food source, even in the presence of larger numbers of fruiting elders, and act as effective seed dispersal agents for bramble, by depositing seeds in a condition and situation that favour the establishment of bramble plants. Therefore, badgers are effective dispersal agents for brambles, and probably other fruits.

While badgers are regarded as moderate dispersers of plants producing fleshy fruits in a Mediterranean setting (Pigozzi 1992; Rosalino *et al*. 2004, 2010), the current study is the first report of this phenomenon in Ireland. It is clear from studies elsewhere that some carnivores achieve seed dispersal, while others do not (Rosalino *et al*. 2004), and it would be useful to distinguish dispersers from non-dispersers in an Irish context.

Limitations of the current study include the fact that the work was carried out in a single year largely at a single site. An assumption is also made that the seeds extracted from fresh badger droppings were comparable to those in the intact fruit and those manually extracted from the ripe fruit. The latter two were obtained from ripe fruits harvested from the latrine and sett areas in the study site (presumable the same stands from which the badgers ate the fruit), while the seeds in treatment (c) were from fresh dung, so that the seeds used in all three treatments were collected within days of one another, and would be at a similar stage of development, assuming that badgers (like most mammals) targeted ripe fruits.

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