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Original article

Seed colour and post-fire bird predation in a Mediterranean pine forest

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Abstract

In a *Pinus halepensis* Mill. forest, a field experiment was designed to evaluate post-fire seed predation as affected by combinations of seed colour and soil substrates: light grey and black seeds combined with light grey ash, dark grey ash and pale brown sand. A survey of bird species inhabiting the area was also carried out and polyphenolic content of seed coat was assessed in seed lots of different colour. Light grey seeds were observed to be less predated on light grey ash, suggesting eucrypsis as a protective strategy against bird predation. On the contrary, no clear pattern was observed for the predation of black seeds on different substrates. In the study area both bird species breaking the seed coat and eating the endosperm and bird species swallowing the whole seed were monitored. We have estimated that more seeds were swallowed than broken, in all colour categories. Light grey seeds, which were found to have a higher content of polyphenols, were predated more than black seeds when exposed on the same substrate. Thus, no evidence was produced that the amount of polyphenols in seed coat could protect seeds from predation.

Keywords: Pinus halepensis; Fire; Seed; Bird interaction; Eucrypsis; Ash; Polyphenols

1. Introduction

In plant species selective pressure by predators relying on visual cues in food searching, such as granivorous birds feeding on the ground, could favour seeds with colours matching the soil substrate. According to Wiens (1978), this type of crypsis can be classified as *eucrypsis*, i.e. the process in which the mimic is similar to the natural background by means of homocromy, countershading or disruptive colouration. In pine species variability of seed colour has been interpreted as an adaptive strategy for coping with post-dispersal predation (Ager and Stettler, 1983; Lanner, 1998). While stable during plant ontogeny (Vidyakin, 2001), seed colour varies among and within populations (Ager and Stettler, 1983; Grzywacz and Rosochacka, 1980; Rosochacka and Grzywacz, 1980; Tillman-Sutela and Kauppi, 1995).

Aleppo pine (*Pinus halepensis* Mill.) is a tree species well adapted to Mediterranean fire-prone environments. It maintains serotinous cones on the crown, i.e. mature cones which do not open in normal environmental conditions; the thermal shock of a fire or the exposure to dry and hot air prompt the cones to open and disperse seeds (Daskalakou and Thanos, 1996; Nathan et al., 1999). On the other hand, seed is an important food source for granivorous birds and seed predation starts few days after fire, when combustion is over and the amount of smoke in the air has declined; 30 days after fire more than 50% of seeds were found to be depleted in the study area (Saracino et al., 1997). In Mediterranean forests fire occurs generally in summer, when populations of birds reach their peak.

In Aleppo pine two seed coat colours have been observed to prevail during the first 2 months after fire, i.e. light grey (light grey spots on a dark grey background), and black seeds; in particular light grey colour prevails in seeds dispersed immediately after fire, while, later in the season, more black seeds are dispersed (Saracino et al., 1997). A mosaic of soil substrates develops after fire, according to fuel load, fire intensity and surface material redistribution. Under tree crowns, where litter accumulation is abundant and combustion temperatures high, light grey ash prevails, mixed with charcoal chips; in canopy gaps, the lower combustion temperatures lead to dark grey ash, rich of carbon particles; as soon as wind erosion and surface runoff occur, uncovered sand patches also develop. In the study area, seeds of differ-

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ent colour could match, at least to some extent, with soil substrates left by fire, namely light grey and black seeds with light and dark grey ashes, respectively. Therefore, post-fire predation could be affected by crypsis effects, reducing the capability of birds to detect seeds.

Seed predation could also be affected by the chemical characteristics of seed coat (Cook et al., 1971). In *Pinus sylvestris*, Rosochacka and Grzywacz (1980) found that seeds of different colours were different in polyphenolic composition; polyphenols have been reported as responsible for both seed colour and seed taste (Hättenschwiler and Vitousek, 2000; Duc et al., 1995).

The aim of this work was to test the hypothesis that in Aleppo pine, seeds of different colours could match with different post-fire soil substrates, in such a way that bird predation rate could be affected. To this aim, two field experiments were performed in the forest: the first one, 1 month after fire, when different substrate patches were large and well differentiated; the second one, 2 months after fire, when substrate patches were smaller, as a consequence of redistribution of burnt material by wind and surface runoff. In particular, in the first experiment we aimed to identify the most protected seed colour on each substrate; in the second experiment we aimed to assess the best protective combination of seed colour and substrate. In the experimental plots, both disturbance by mammals and interference by shrub resprouts was prevented. Polyphenolic composition was also assessed according to seed colour, to rule out its possible effect on seed palatability and bird predation rates.

2. Materials and methods

2.1. Study site and experimental areas

The experiment was carried out in a mature Aleppo pine forest growing on alluvial sandy dunes close to the Ionian sea, Southern Italy (40°30′20″N, 17°00′08″E; average rainfall, 535 mm; mean annual temperature, 15.8 °C; height of trees, 12–14 m; main understorey shrub species, *Phillyrea angustifolia* L. and *Pistacia lentiscus* L.). On June 15th 1997, a fire burnt the forest over an area of about 150 ha, leaving large areas where trees were ‘charred’ (needles, twigs and some cones completely burnt), as well as smaller areas where trees were only ‘scorched’ (only needles damaged but not completely burnt).

On July 1st 1997, three experimental areas (7 × 5.5 m) were established in a ‘charred’ stand, where recolonisation by birds normally takes place rather soon after fire (Saracino et al., 1997). Experimental areas were located: under the crown of a charred tree, with light grey ash as prevailing substrate (area 1); 5 m distant from the charred tree, with dark grey ash as prevailing substrate (area 2); 10 m distant from the other two areas, with pale brown sand as prevailing substrate (area 3).

To prevent disturbance by mammals, each area was surrounded by a metal fence, 1.5 m high, 0.5 × 0.5 cm mesh, fixed at a depth of 20 cm into the soil, with the upper edge bent outwards. Six rodent traps were placed in each area: no rodent was captured throughout the experiment. Experimental areas were kept clear from shrub resprouts throughout the experiment. Herbaceous plants were not present. Within each area, 6–12 experimental plots were randomly assigned to treatments (combination of seed and substrate colours) in the predation experiments (see below). Plots were 0.5 × 0.5 m plastic cardboards, at least 1 m away from the fence, with 5 cm high lateral wood walls; when in place, walls were at the ground level. Each plot was filled with 5 cm of experimental substrates.

2.2. Seeds

Seeds were extracted from cones collected on 10 Aleppo pine trees, growing close to the study area; five ‘grey’ old (serotinous) cones and five ‘brown’, still closed, mature cones were gathered from the crown of each tree. Cones were allowed to open in the oven at 60 °C for 24 h and seeds extracted. After extraction, two seed lots homogeneous for colour (light grey, seed lot 1; black, seed lot 2) were prepared and seed colour assessed according to the Munsell notation of *Hue, Value* and *Chroma*. The *Hue* notation of a colour indicates its relation to red, yellow, green, blue and purple; the *Value* notation indicates its lightness; the *Chroma* notation indicates its strength (Munsell Color, 1994). Colour attribution was made by the same person under the same light conditions. From each seed lot, 150 seeds were sampled and the following traits assessed: percentage of empty seeds, by easy gravimetric separation from full seeds, full seed weight, seed coat weight (Table 1). Only full seeds were exposed to predation.

2.3. Polyphenolic content of seed coat

Polyphenolic composition of seed coat was assessed on 50 seeds sampled from ‘light grey ’ and ‘black’ seed lots. By mean of a razor blade, coats were separated from the en-

Table 1
Seed lots (n = 150) used in predation experiments; standard deviation (S.D.) in brackets

Colour	Munsell notation	Full seed weight (mg)	Seed coat weight (mg)	Seed coat weight (% of seed weight)	Empty seed (%)
1. Light grey	10YR 5/1	20.9 (4.8)	6.3 (1.4)	33.43	7
2. Black	5YR 2.5/1	19.3 (4.6)	6.4 (1.8)	36.60	29
		***	n.s.	***	

Asterisks indicate significant differences at $P < 0.05$ according to independent samples t-test; n.s. means not significant at $P < 0.05$.

dosperm, then finely ground. Polyphenolic content was determined by the Folin–Denis method (King and Heath, 1967) and expressed as tannic acid equivalents (in % of d.w.), by comparison with a tannic acid standard. Seed palatability should be evaluated taking into account the different feeding habit of granivorous birds. Therefore, two extraction solutions were used: NaCl solution (0.8% v/v), which extracts only water soluble polyphenols, was used to simulate the saliva effect of seed-breaking birds; pure ethanol, which extracts all polyphenols in the sample, was used to simulate the process occurring in the gizzard of birds who swallow the entire seed. Indeed, Fringillidae and Ploceidae species, inhabiting the study area, break the seed coat and eat the endosperm (Newton, 1967), whereas other bird species, such as Columbidae and Corvidae, swallow the whole seed (Vander Wall and Balda, 1981; Lanner, 1998). In Aleppo pine the seed coat is soft, so seeds are not dispersed after ingestion.

2.4. Substrates

The substrates available in experimental areas (i.e. light grey ash, substrate 1; very dark grey ash, substrate 2; and pale brown sand, substrate 3) were used in experimental plots. Substrates were sieved to remove seed coat remnants and wood debris and assessed for colour according to Munsell's notation (Munsell Color, 1994) (Table 2).

2.5. Predation experiments

In each experimental plot, full seeds were exposed to predation placing a regular grid (8.3 × 4.5 cm) with small holes on the substrate. Fifty chromatically homogenous seeds were exposed in each plot in order to simulate the post-fire seed dispersal rate (≈200 seeds per m^2), previously observed in a charred stand (Saracino et al., 1997). Seed wings were removed and seeds exposed with their convex side upward, preventing them from sinking into the substrate. Each experiment lasted 24 h, starting at 16:00 h. In burnt pine stands, birds feeding activity tends to concentrate in the early morning and late afternoon during summer. At the end of each experiment, the substrate was sieved to collect intact seeds and seed coat fragments. In the laboratory, we carefully inspected fragments to estimate the number of seeds that were damaged (broken) by seed-breaking birds; the difference between the number of seeds initially exposed and the number of 'broken' seeds was considered as an estimate of the number of seeds predated 'as a whole' (swallowed seeds) by bird species. Some bird species are known to use a 'mixed' feeding technique, i.e. they can remove the seed and then break it somewhere far away. However, in the study area, this technique is probably restricted to *Parus major* (see Snow and Snow, 1988), which shows the lowest abundance in the area (Table 3).

Table 2
Substrates used in experimental plots

Substrate and colour name	Munsell notation [a]
1. Light grey ash	7/N
2. Very dark grey ash	7.5YR 3/1
3. Pale brown sand	10YR 6/3

[a] Determined on dry substrates.

Two experiments were performed, with the following design:

- Experiment 1, 30 days after fire. Both seed lots (light grey and black seeds) on substrate 1 (light grey ash) in experimental area 1, on substrate 2 (very dark grey ash) in experimental area 2, on substrate 3 (pale brown sand) in experimental area 3; three replicates for each colour in each area (six plots per area).
- Experiment 2, 60 days after fire. Both seed lots (light grey and black seeds) on substrate 1, 2 and 3 in all experimental areas; two replicates for each seed/substrate combination in each area (12 plots per area).

Note that in experiment 1 the substrates in experimental plots were the same as in the surrounding experimental areas, so that predation was assessed in a chromatically homogeneous substrate. On the other hand, in experiment 2, soil conditions were much more patchy due to redistribution of surface burnt material and different types of substrates were used in each area, so that predation was assessed in a chromatically heterogeneous substrate.

2.6. Survey of bird species

A survey of granivorous birds inhabiting the burnt area was carried out at 06:00 h during one calm day in July and one calm day in August, soon after the end of the experiments. The '20 min' point count method, inspired by Blondel et al. (1970), with observation radius of 50 m and permanent centre inside the experimental site, was applied to document the species present in the area. Relative abundances of bird species were determined by visual and auditory contacts (a relative abundance of 1 was attributed to each contact). This method is likely to underestimate the density of birds feeding

Table 3
Relative abundances of bird species, grouped according to feeding habit, in the study area: highest single counts of individuals of bird species registered during the two surveys

Swallowing species	
Columba palumbus	1
Streptopelia turtur	1
Pica pica	3
Seed-breaking species	
Parus major	1
Passer domesticus	8
Passer montanus	5
Fringilla coelebs	4
Serinus serinus	4
Carduelis chloris	3
Carduelis carduelis	4

in flocks on the ground. Tracks of *Columba palumbus, Pica pica* and other passerine birds (Brown et al., 1987) observed in the experimental plots before seed collection substantially confirmed the results of acoustic counts.

2.7. Statistical analyses

Percentages of seeds predated (broken, swallowed and total) in each experimental plot underwent arcsine square root transformation before the analysis; the homogeneity of variance and the normal distribution of residuals were also assessed. In experiment 1, differences in total seed predation between seed colour categories were compared by means of an independent-samples *t*-test ($P < 0.05$), within each substrate. Data from experiment 2 were analysed by means of a mixed ANOVA model, in which experimental areas were treated as random blocks, whilst seed and substrate colours were treated as fixed factors, in a factorially-crossed design (split-block design, see Steel and Torrie, 1981). All statistics were performed using the SAS statistical package (SAS Institute Inc., 1990).

3. Results

3.1. Predation on a homogeneous substrate

In experiment 1, grey seeds were predated more than black seeds on dark grey ash ($t = 6.22$, $P = 0.003$; df = 4) and pale brown sand ($t = 3.42$, $P = 0.042$; df = 4); on the contrary, predation rates were not significantly different on light grey ash ($t = 1.84$, $P = 0.140$; df = 4) (Fig. 1).

3.2. Predation on a heterogeneous substrate

In experiment 2, significant differences in the percentage of total seed predation were observed between seed lots ($F_{1,2} = 22.23$, $P = 0.0422$) and substrates ($F_{2,4} = 16.16$, $P = 0.0121$). Consumption of grey seeds was significantly lower ($P < 0.05$) on light grey ash than on very dark grey ash and pale brown sand (Fig. 2). Similar results were found for black seeds, whose predation was significantly lower ($P < 0.05$) on light grey ash than on very dark grey ash and sand (Fig. 2).

Grey seeds were predated more than black seeds on all substrates: light grey ash ($t = 2.58$, $P = 0.028$; df = 10), very dark grey ash ($t = 3.86$, $P = 0.003$; df = 10) and pale brown sand ($t = 3.67$, $P = 0.004$; df = 10).

3.3. Feeding habit, seed colour and polyphenolic content

According to feeding habit reported in Table 3, bird species, which break the seed coat and eat the endosperm were estimated to be more frequent in the study area than species which swallow the whole seed. Nevertheless, when data from the two experiments were pooled together, whole seed swallowing accounted for a higher proportion of seed consumption than seed-breaking, both on all substrates and in all seed colour categories (Fig. 3). Percentage of broken seeds was not significantly different between seed colour categories ($P = 0.160$, according to independent samples *t*-test) and among substrates ($P = 0.486$ according to one-way ANOVA) (Fig. 3a, b). As for swallowed seeds, on the contrary, predation was different between seed lots ($P < 0.0001$ according to independent samples *t*-test) and substrates ($P = 0.003$ according to one-way ANOVA). Black seeds were swallowed less than grey seeds and swallowing was significantly lower ($P < 0.05$) on light grey ash than on very dark grey ash and sand (Fig. 3a, b) for both seed lots. No significant difference in polyphenolic content was found between seed lots in case of NaCl extraction ($P = 0.311$); extraction in ethanol showed a significantly higher polyphenolic content in grey than in black seeds ($t = 6.73$, $P = 0.003$, df = 4) (Fig. 4).

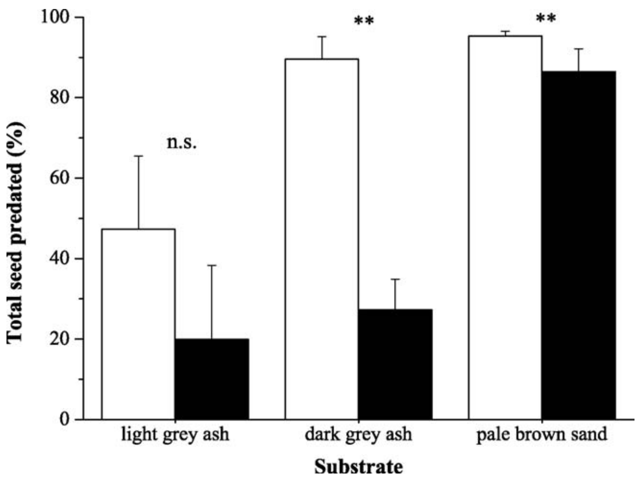

Fig. 1. Predation on a homogeneous substrate (experiment 1). Predation (mean ± S.D.) of grey (empty columns) and black (black columns) seeds on different types of substrates. * = significant ($P < 0.01$) differences between seed colours within each substrate type, according to independent samples *t*-test; n.s. = not significant.

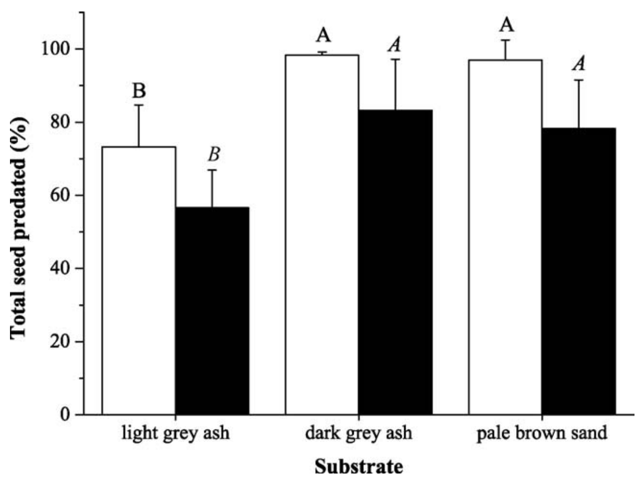

Fig. 2. Predation on a heterogeneous substrate (experiment 2). Predation (mean ± S.D.) of grey (empty columns) and black (black columns) seeds on different types of substrates. Different capital letters indicate significant ($P < 0.05$) differences among substrate types within each seed colour category, according to Duncan's multiple range test.

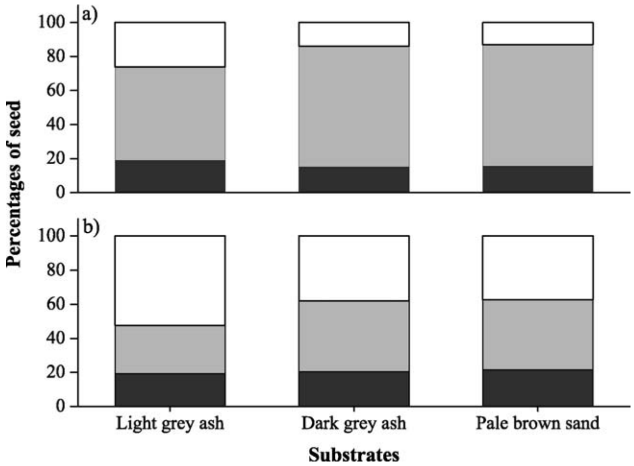

Fig. 3. Percentages of seeds broken (dark grey columns), swallowed (light grey columns) and left (empty columns) according to substrate categories for light grey seeds (upper panel, a) and black seeds (lower panel, b), respectively.

4. Discussion

Seeds laying on the ground may be protected from bird predation either by homochromy with the substrate (eucrypsis) or by the so-called 'disruptive' colouration, i.e. spots of contrasting colours, which is known to interrupt the visual cue image of birds (Endler, 1978; Wiens, 1978). In our experiments, grey seeds displayed good chromatic matching with light grey ash as well as disruptive colouration on dark grey ash and pale brown sand.

In experiment 2, i.e. on a chromatically heterogeneous substrate, grey seeds were found to be less predated on light grey ash, thus suggesting that eucrypsis was at work as protective strategy. The same protection strategy seems to emerge from experiment 1, on a chromatically homogeneous substrate. As for black seeds, experiment 1, in which they were predated less on ashes than on sand, may suggest crypsis or colour matching with charcoal chips; on the heterogeneous substrate, on the contrary, a lower seed consumption with respect to sand was observed only on light grey ash.

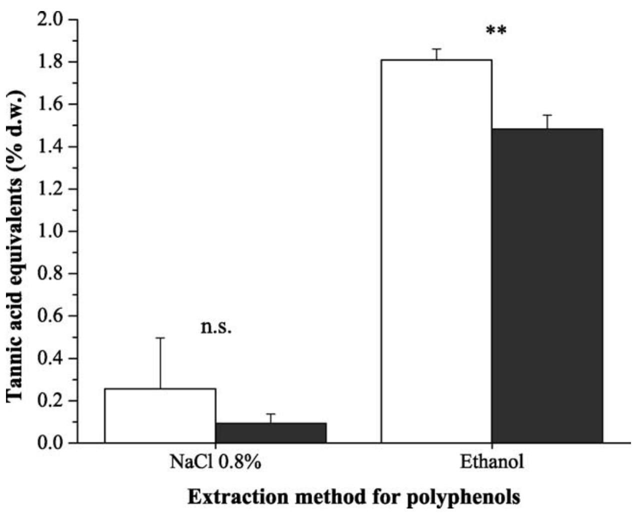

Fig. 4. Polyphenolic content (expressed as tannic acid equivalent) (mean ± S.D.) of light grey (empty columns) and black (grey columns) seeds with NaCl (0.8%) and ethanol extraction methods; ** = significant ($P < 0.01$) differences based on independent samples *t*-test; n.s. = not significant.

On the other hand, when interpreting these patterns, it should be considered that the matching of seed colour and substrate may be perceived in a different way by human and bird eyes (Whittingham and Markland, 2002). Indeed, sensitivity in UV region is widely reported to be important for birds foraging activity (Bennett and Cuthill, 1994; Tovée, 1995; Church et al., 2001; Maddocks et al., 2001; Honkavaara et al., 2002). Moreover, since in the experimental plots the seeds had been always placed on the substrate so as to be well visible and accessible, predation on light grey ash substrate could have been slightly overestimated with respect to natural conditions. Indeed, seeds which are immediately dispersed after fire, tend to sink into the thick and soft ash layer (Saracino and Leone, 1993), thus becoming less accessible to birds, who show low scratching ability in searching food (Whalen and Watts, 2000).

The higher consumption of grey seeds relative to black seeds, in both experiments and on all substrates (with the only exception of light grey ash in experiment 1), cannot be explained by crypsis and/or by differences in seed characteristics, as reported in Table 1. On the contrary, differences in seed coat roughness might have played a role. Indeed, TEM images (not shown) confirmed that in Aleppo pine, as in other conifer species (Vidyakin, 2001), seeds appear black because their coat is covered by a granular layer, containing a black pigment, which causes black seeds to be more rough than grey seeds. Pank (1976) observed that palatability of *Pseudotsuga menziesii* seeds by several bird species decreased after chemical treatments, which increased seed surface roughness.

According to feeding habit, summarised in Table 3, the evidence that seed swallowing birds consumed a higher proportion of seeds (Fig. 3) could be explained considering the higher energetic requirement of bird species with a larger body size, as seed swallowing species are. We have to recognise that the proportion of swallowed seeds could have been slightly overestimated, due to the presence of birds like *P. major* that remove seeds and break them at some distance in the area, as specified in the methods. On the contrary, we are quite confident in excluding that ant predation might have significantly affected our estimates, since no ant colonies have been observed in the area.

Also, a hierarchic access to food (first large birds, then small ones) cannot be excluded. In any case, different visual acuity can affect foraging efficiency of differently sized species (Endler, 1978), while coexistence of different foraging strategies may suggest mechanisms allowing niche separation between bird species (Whalen and Watts, 2000).

More grey than black seeds were predated by swallowing birds (Fig. 3), thus suggesting that roughness of black seeds could affect feeding preferences of those birds. Grey seeds showed a higher content of total polyphenols. Therefore, no evidence emerged from our data that polyphenols may represent an unpalatable substance for swallowing birds, protecting seeds from predation; however, we cannot exclude that differences in the qualitative polyphenolic composition could play a role, as documented by Rosochacka and Grzywacz (1980) for *P. sylvestris*. Differences in polyphenolic content between seeds of different colour have been reported in literature (Grzywacz and Rosochacka, 1980; Rosochacka and Grzywacz, 1980). In particular, in *P. sylvestris* Tillman-Sutela et al. (1998) found that phenolic extracts have a lower reflectance in the UV region for dark than for light colours. As previously stated, UV vision sensitivity, varying among bird species (Chen and Goldsmith, 1986; Osorio et al., 1999), plays an important role in birds foraging activity. Further work is clearly needed to fully untangle interactions between chemical composition, detectability and seed predation.

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