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The role of great apes in seed dispersal of the tropical forest tree species *Dacryodes normandii* (Burseraceae) in Gabon

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Abstract: The identification of seed dispersers and predators is essential to understand the effect of anthropogenic disturbances, and the associated defaunation process, on tropical forest dynamics in Central Africa. In this study, the animals involved in seed predation and dispersal of *Dacryodes normandii* (Burseraceae), an endozoochorously dispersed tree species endemic to Gabonese forests, were identified in a site in south-east Gabon using two complementary methods: direct observation and camera-trap monitoring of fruit piles. The combined sampling effort (172 h of direct observations and 796 d of camera trapping) led to the identification of six disperser and eight predator species of *D. normandii* seeds. With high frequency of consumption (88% and 57% of their visits, respectively) and long visit duration (83 and 23 min, respectively), the western lowland gorilla and central chimpanzee were identified as the main dispersers of this species. Seeds passed through the gorilla gut exhibited high germination success (68%). Rodents were identified as predators of *D. normandii* seeds, potentially displaying rare secondary dispersal through scatter-hoarding. The results of this study highlight the importance of great apes in the seed dispersal of this tree species.

Key Words: Africa, frugivory, *Gorilla gorilla gorilla*, logged forest, *Pan troglodytes troglodytes*, primates, seed dispersal, seed predation, tropical rain forest

INTRODUCTION

Animal-dispersed plant species interact with a cohort of frugivores, whose roles regarding population dynamics depend on their specific characteristics. The number of seeds dispersed by an animal species is linked to the importance of fruits in its diet, as well as its food preferences (Schupp 1993). Both factors influence the frequency of consumption of a given plant species, and ultimately seed dispersal quantity (Schupp 1993). Seed processing in the mouth and gut might alter seed germination potential, and therefore hamper the dispersal services provided by a given frugivore (Schupp 1993). The action of granivorous species as predators, or scatter-hoarding dispersers, might also influence seed fate (Schupp 1993). As the disperser's characteristics influence seed dispersal effectiveness, fruit features determine which animals consume a plant species (Gautier-Hion *et al*. 1985) and therefore its community of dispersers. It is important to study the role of mammals in the regeneration processes of animal-dispersed plant species in order to assess the impacts of the phenomenon of 'defaunation' (Galetti & Dirzo 2013, Kurten 2013). Large mammals are thought to be effective dispersers, but are also disproportionately affected by anthropogenic pressure (Linder & Oates 2011, Wright 2003). Central African great apes (western gorilla, *Gorilla gorilla*; chimpanzee, *Pan troglodytes* Blumenbach; and bonobo, *Pan paniscus* Schwartz) are a good example of such species. Great apes are important dispersers because of their highly frugivorous diet, large body mass and extended home

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range (Beaune *et al.* 2013a, Poulsen *et al.* 2001, Tutin 2001, Voysey *et al.* 1999).

This study took place in a logged forest in Gabon. Among the dominant plant families found in Gabonese forests, species of the family Burseraceae are characterized by a high level of endemism (Aubréville 1962, Doucet 2003). Those belonging to the genera *Dacryodes*, *Canarium* and *Santiria*, which provide important timber and/or non-timber forest products (Aubréville 1962, Doucet 2003), are zoochorous and are consumed by the endangered great apes (Tutin & Fernandez 1993, Tutin *et al.* 1991, Williamson *et al.* 1990). But the main seed dispersers of these plant species are not known; neither is their exact influence on plant fitness.

The objective of this work was to describe the respective roles of vertebrates involved in the seed dispersal and predation of a poorly known zoochorous tree species endemic to Gabon, *Dacryodes normandii* Aubrév. & Pellegr. (Burseraceae), and to assess their importance in the dispersal process. We tested the following two hypotheses. (1) Considering that *D. normandii* fruit can be categorized in the bird-monkey syndrome (Gautier-Hion *et al.* 1985), large birds and monkeys will be dispersers of its seeds. However, we expect large mammals to provide important dispersal services to this species. In particular, great apes will be the main dispersers of this species in terms of the quantity of dispersed seeds and the high quality of seed treatment in their mouth and gut. (2) Large rodents will be mainly involved in seed predation (Hecketsweiler 1992), but considering their scatter-hoarding behaviour, they will occasionally disperse *D. normandii* seeds.

METHODOLOGY

Study site

This study was carried out in a sustainably managed and certified (Forest Stewardship Council) logging concession in south-east Gabon (0°30′–1°00′ S, 12°30′–14°00′ E) from December 2013 to March 2014. The study area covers 617 000 ha and the vegetation mostly comprises moist tropical evergreen forest. It is an old secondary forest as characterized by White (1986), dominated by *Scyphocephalium ochocoa* Ward (Myristicaceae) and *Aucoumea klaineana* Pierre (Burseraceae) (Demarquez & Jeanmart unpubl. data, White 1986). In similar forests in central Gabon, it has been shown that about 60% of tree species are dispersed through endozoochory (Doucet 2003). Western lowland gorilla (*Gorilla gorilla gorilla* Savage & Wyman) and central chimpanzee (*Pan troglodytes troglodytes* Blumenbach) coexist sympatrically within the study site. The climate is equatorial with an average annual rainfall of 1700 mm (Moupela *et al.* 2013), with two seasons of heavy precipitation (March–May and September–December) and two seasons of lower precipitation. The average annual temperature is 26°C (Moupela *et al.* 2013), with the highest temperatures being recorded from February to April, and the lowest in July and August.

Study species

Dacryodes normandii is a medium to large canopy tree, endemic to the evergreen forests of Gabon (Doucet 2003). It provides timber and non-timber forest products (Aubréville 1962). It has intermediate light requirements, as it tolerates shade at seedling stage but becomes light-demanding when mature (Doucet 2003). *Dacryodes normandii* is dioecious and female trees produce obovoid drupes of 3.5 cm in length, black/purple in colour, with a thin exocarp and a sweet-sugary, juicy and soft pulp (Aubréville 1962). Fruiting is observed for trees from 13 cm dbh (Doucet 2003). Fruit production is defined as supra-annual, occurring at intervals longer than 1 y (Fourrier 2013). Flowering takes place from September to November and fruits are produced from October to February (Aubréville 1962, Doucet 2003, Fourrier 2013, Hecketsweiler 1992). Fruits are available for 1.6 mo on average (Fourrier 2013). Within the study site and during the study period, unripe fruits were observed in December, and ripened from January to February (B. Haurez, pers. obs.). The average density of *Dacryodes normandii* in the study site is 54.8 stems km^{-2} (for dbh > 20 cm) (Demarquez & Jeanmart unpubl. data).

Identification and contribution of vertebrate seed dispersers

Direct observations. In December 2013, six mature trees of *Dacryodes normandii* with the main part of the crown visible from the ground (hereafter referred to as focal trees), were visited and examined for signs of fruiting (mainly unripe fruits in the canopy and on the ground). In order to ensure independence of observations, focal trees were located at least 1 km apart (Babweteera & Brown 2009). Observations were made with binoculars between 06h30 and 17h30 in periods of availability of both unripe and ripe fruits (from mid-December to end of February). Observers were hidden in a position providing the best visibility of the focal tree canopy. For all vertebrate visits to focal trees the following information was recorded: animal species; feeding behaviour when eating fruits and/or seeds (Chapman & Chapman 1996, Kitamura *et al.* 2006); time and duration of visits; and number of animals observed (Kitamura *et al.* 2006). Sampling effort was defined as the number of observation hours.

Camera trapping. Camera traps (GameSpy Moultrie M-80XT, approximate detection range 13.5 ± 1.5 m) were installed beneath 10 mature fruiting trees, located at least 1 km from each other (Babweteera & Brown 2009). A pile of fresh *Dacryodes normandii* fruits was placed in front of the camera to attract frugivores (adapted from Babweteera & Brown 2009, Kitamura *et al.* 2006, Moupela *et al.* 2013, Seufert *et al.* 2009). Cameras were monitored weekly from December 2013 to March 2014. They were automatically activated any time a movement occurred within the range of the detector. An independent visit was defined as (1) consecutive records of individuals of different species, (2) non-consecutive records of individuals of the same species, and (3) consecutive records of individuals of the same species taken more than 30 min apart (O'Brien *et al.* 2003). For all independent visits, the following data were recorded: animal species, feeding behaviour when applicable, time and duration of visits, and the number of animals detected (Chapman & Chapman 1996, Kitamura *et al.* 2006). Sampling effort was defined as the number of trap days, i.e. the number of active cameras multiplied by the number of operating days (24 h).

Role of great apes and rodents. To determine the fate of fruits and seeds of *Dacryodes normandii* potentially removed by terrestrial rodents, rodent burrows were sought in the vicinity of four of the focal trees. Twenty-one burrows were found and excavated and seeds were counted and identified to the most precise taxonomic level. Their status was recorded ('intact' when the seed was undamaged, and 'predated' when the seed was broken or rotten and the embryo eaten).

Fresh gorilla faeces collected at nest sites were inspected to investigate the presence of *Dacryodes normandii* seeds during the fruiting period (January–February) in 2012 and 2014. A total of 49 faecal units were analysed. Seed viability after gut passage was assessed through germination trials under the same conditions in both years in a nursery at the study site (n = 53 gut passed seeds). A control treatment, involving seeds extracted from *Dacryodes normandii* fresh fruits and cleaned from pulp (n = 64 control seeds), was also realized. Seeds were sown individually in soil collected from the study site. The nursery was watered on a daily basis. Germination trials involving seeds collected in chimpanzee faeces were not performed because of the complexity of identifying chimpanzee faeces with certainty.

Data analysis

All photographed or directly observed mammal species were identified following Kingdon (1997) and birds using Serle & Morel (1993). On pictures where only parts of the animals' bodies were visible, they were identified to the most precise taxonomic level possible or classified as 'undetermined'. Additionally, to avoid incorrect identifications, all red duiker species (*Cephalophus callipygus* Peters, *C. dorsalis* Gray, *C. nigrifrons* Gray, *C. leucogaster* Gray, *C. ogilbyi* Waterhouse) were collectively classified as *Cephalophus* spp.

The duration of visits involving consumption was calculated as the time difference between arrival and departure of the animal directly observed, or the time between the first and last photographs of the visit. As the relative amount of fruit consumed, a component of dispersal effectiveness, is influenced by the frequency of visits and their duration (Schupp 1993), an index of fruit consumption, I_{FC} was computed as follows (adapted from Moupela *et al.* 2013):

$$I_{FC} = (N_{obs.cons}/N_{obs.})\,D \qquad (1)$$

with $N_{obs.cons}$ = number of observations of a given species involving consumption of fruits, N_{obs} = total number of observations of this species, and D = mean length of visit involving consumption of fruits. The ecological functions of different animal species were determined using the information provided by pictures and fruit remnants, as well as from existing literature. Animals were classified into four categories (adapted from Gautier-Hion *et al.* 1985 and Moupela *et al.* 2013): (1) predator: those that destroy the seeds; (2) disperser: those that consume fruits while leaving seeds intact and removing them from the vicinity of the parent trees; and (3) neutral: those that show no interest in *D. normandii* fruits. All species displaying null I_{FC} were considered neutral.

The effect of passage in gorilla gut on seed germination was evaluated through the comparison of germination success of gut-passed seeds with that of control seeds, with a χ^2 test.

RESULTS

Identification and contribution of seed dispersers

In 172 h of direct observations, three species of *Dacryodes normandii* disperser were identified: one arboreal primate, the putty-nosed monkey (*Cercopithecus nictitans nictitans*), and two large birds, the white-crested hornbill (*Tropicranus albocristatus*) and the great blue turaco (*Corythaeola cristata*) (Table 1).

In a total of 796 camera-trap days, 572 vertebrate detection events occurred (97.2% involving mammals, 1.7% birds and 1.1% undetermined). Twenty-six species or groups of species were identified from camera-trap pictures, accounting for 71.3% of detection events. The remaining 28.7% involved undetermined animals, mostly Muridae (24.0%). Three of the identified species acted predominantly as seed dispersers: two great apes,

Table 1. Animal species involved in consumption events during direct and indirect observations of *Dacryodes normandii* trees in a Gabonese logging concession from December 2013 to March 2014, ordered by I_{FC}. $N_{obs.cons}$ = number of observations of a given species involving consumption of fruits, N_{obs} = total number of observations of this species and D = mean length of visit involving consumption of fruits, $I_{FC} = (N_{obs.cons}/N_{obs.})$ D.

Species	Common name	N_{obs}	$N_{obs.cons}$	D (min)	I_{FC}	Role
Gorilla gorilla gorilla Savage & Wyman	Western lowland gorilla	8	7	85	74	Disperser
Pan troglodytes troglodytes Blumenbach	Central chimpanzee	7	4	23	13	Disperser
Cercopithecus nictitans nictitans L.	Putty-nosed monkey	2	2	5	5.0	Disperser
Tropicranus albocristatus Cassin	White-crested hornbill	1	1	3	3.0	Disperser
Funisciurus pyrropus Cuvier	Fire-footed rope squirrel	7	1	6	0.86	Predator, disperser (occasional through scatter-hoarding or dropping during transport)
Corythaeola cristata Vieill.	Great blue turaco	3	2	1	0.67	Disperser
Cephalophus silvicultor Afzelius	Yellow-backed duiker	28	3	3	0.32	Predator
Artherurus africanus Gray	Brush-tailed porcupine	33	2	5	0.30	Predator, disperser (occasional through scatter-hoarding or dropping during transport)
Epixerus ebii Temminck	Ebian palm squirrel	25	3	2	0.24	Predator, disperser (occasional through scatter-hoarding or dropping during transport)
Loxodonta cyclotis Matschie	African forest elephant	39	5	1	0.13	Disperser
Cricetomys emini Wroughton	Giant pouched rat	35	2	1	0.057	Predator, disperser (occasional through scatter-hoarding or dropping during transport)
Cephalophus spp.	Red duiker	101	5	1	0.050	Predator
Funisciurus isabella Gray	Lady Burton's rope squirrel	65	1	1	0.015	Predator, disperser (occasional through scatter-hoarding or dropping during transport)
Undetermined Muridae	Murid	137	1	1	0.0073	Predator, disperser (occasional through scatter-hoarding or dropping during transport)

the western lowland gorilla and the central chimpanzee, and the African forest elephant (*Loxodonta cyclotis*, Proboscidea) (Table 1). Both great ape species frequently consumed *D. normandii* fruits and their consumption events were relatively long, resulting in the highest I_{FC} observed (74 and 13 respectively). Elephants less frequently consumed *D. normandii* fruits and their visits were much shorter (I_{FC} of 0.13).

The remaining species (n = 8) observed to interact with *D. normandii* fruits were likely to act mainly as predators. They were involved less frequently in consumption events and their visits were consistently shorter than 10 min ($I_{FC} = 0.86–0.0073$) (Table 1).

Role of great apes and rodents. No *D. normandii* seeds were found in the 21 prospected rodent burrows (mean depth ± SD = 36 ± 10 cm, range = 20–70 cm). Two destroyed seeds of another species of Burseraceae (*Santiria trimera* (Oliv.) Aubrév.) were found (Appendix 1). These results support the evidence that terrestrial rodents are mainly predators of *D. normandii* and that dispersal events through scatter-hoarding are likely to be rare.

We observed that 18% of fresh gorilla faeces analysed (n = 49) contained *D. normandii* seeds (number of seeds = 170, mean number of seeds per faecal sample ± SD = 18.9 ± 14.4, range = 0–49), which exhibited a germination success of 68% (n = 53 seeds sown). The germination success displayed by seeds passed through the gorilla gut was not significantly different from that of seeds extracted from fresh fruits (n = 164 seeds sown, mean germination success = 73%) (df = 1, $\chi^2 = 0.74$, P = 0.39).

DISCUSSION

Owing to direct and indirect observations, the present study identified six disperser species of *Dacryodes normandii*, among which primates were the most important. In particular, supported by I_{FC} high values, great apes are likely to be the main dispersers of this species. Rodents, squirrels and duikers are mainly predators of *D. normandii* seeds.

Importance of great apes in seed dispersal of *Dacryodes normandii*

Among primate species, the western lowland gorilla is considered a very effective seed disperser (Haurez *et al.* 2013, Petre *et al.* 2013, Tutin *et al.* 1991) and an essential actor in forest dynamics and maintenance of forest structure (Tutin 2001). Seeds dispersed by gorillas are generally viable (Petre *et al.* 2015, Poulsen *et al.* 2001, Voysey *et al.* 1999). The high germination success displayed by seeds of *D. normandii* collected in gorilla faeces (68%), which does not differ from that of unpassed seeds, attests to their preservation during gut passage. In other sites, consumption of *D. normandii* fruits has already been reported (Fourrier 2013, Tutin & Fernandez 1993, Tutin *et al.* 1991, Williamson *et al.* 1990). Since gorillas exhibit (1) a high frequency of visiting fruiting *D. normandii* trees, (2) long visit durations in cases of consumption, and (3) the consumption of a large number of fruits at each visit, they may provide reliable dispersal services for this tree species. Furthermore, more than 50% of gorilla dung is deposited at nest sites (Todd *et al.* 2008) and gorillas preferentially select open habitats for nesting (Haurez *et al.* 2014, Petre *et al.* 2015, Tutin *et al.* 1995, Willie *et al.* 2012), which offer suitable conditions for seed germination and seedling growth (Rogers *et al.* 1998, Tutin *et al.* 1991, Voysey *et al.* 1999). *Dacryodes normandii* has intermediate light requirements (Doucet 2003), therefore suggesting that its seeds and seedlings may benefit from the light conditions characteristic of gorilla nest sites (Rogers *et al.* 1998, Tutin *et al.* 1991, Voysey *et al.* 1999). As a consequence, gorilla may provide directed dispersal for *D. normandii* (Howe & Smallwood 1982), as has been observed for other plant species with different degrees of shade tolerance (from high tolerance to shade intolerance) (Petre *et al.* 2015, Voysey *et al.* 1999). However, the fate of gorilla-deposited seeds of *D. normandii* is still largely unknown. A study encompassing all stages from faecal deposition to sapling recruitment may help to reliably assess the likely importance of gorillas in the regeneration of *D. normandii*.

The chimpanzee is considered a high-quality disperser (Gross-Camp & Kaplin 2011), displaying seed swallowing, spitting and wadging behaviours, depending on the plant species (Chapman & Russo 2005, Gross-Camp & Kaplin 2005, 2011; Lambert 1999). Chimpanzees generally disperse viable seeds (Wrangham *et al.* 1994), although their impact on germination potential depends on the taxon considered (Gross-Camp & Kaplin 2005). *Dacryodes normandii* pulp is a valuable food resource for the chimpanzee in Gabon, and its seeds are commonly observed in chimpanzee faeces (Tutin & Fernandez 1993). However, data on the disperser effectiveness of chimpanzee for this species are lacking.

Other dispersers and predators of *Dacryodes normandii*

Medium- and small-sized primates, for example *Cercopithecus* spp. (Gautier-Hion *et al.* 1980, Lambert 1999), are important dispersers (Chapman & Russo 2005, Poulsen *et al.* 2001), dispersing seeds through defecation and spitting (Chapman & Russo 2005). The present study highlights a role in *D. normandii* seed dispersal for the putty-nosed monkey (*C. n. nictitans*). This species is known to consume the fruit pulp of five species of Burseraceae that share fruit characteristics with *D. normandii* (Gautier-Hion *et al.* 1980, Poulsen *et al.* 2001, 2002), and *Santiria trimera* seeds exhibit enhanced germination after dispersal by this monkey (Poulsen *et al.* 2001).

The role of the African forest elephant in seed dispersal is well documented (Blake *et al.* 2009, Campos-Arceiz & Blake 2011). The elephant consumes *D. normandii* fruits, without destroying their seeds, as evidenced by the presence of whole seeds in dung (Feer 1995a, Fourrier 2013), and can therefore be considered as a disperser of this species (Gautier-Hion *et al.* 1985). However, considering their low I_{FC} (0.13) and the fact that, based on camera-trap observations, they appear to only consume *D. normandii* opportunistically while moving, their role is likely to be of lesser importance.

Dacryodes normandii belongs to one of the three most important families for specialized avian frugivores (Snow 1981). The present study has suggested a dispersal role for the white-crested hornbill (*Tropicranus albocristatus*) and the great blue turaco (*Corythaeola cristata*), even though the overall number of observations of birds feeding on *D. normandii* was surprisingly low. Turacos and hornbills are endozoochorous dispersers, as passage through their gizzards does not destroy seeds (Gautier-Hion *et al.* 1985).

Three squirrels (*Funisciurus pyrropus, F. isabella* and *Epixerus ebii*), two species of terrestrial rodents (*Atherurus africanus* and *Cricetomys emini*) and one undetermined Muridae were observed to handle *D. normandii* fruits. All these taxa are predominantly seed predators (Beaune *et al.* 2013b, Emmons 1980, Gautier-Hion *et al.* 1985), but may contribute to short-distance dispersal through food hoarding and seed dropping during transport to and from the cache (Emmons 1980, Gautier-Hion *et al.* 1985, Moupela *et al.* 2013). However, as no seed of *D. normandii* was found in the prospected burrows, these dispersal events are thought to be rare.

Fallen fruits are an important food resource for duikers (Seufert *et al.* 2009). *Cephalophus* spp. have been shown to act both as seed dispersers (mostly for species with medium-sized fruit and hard stones) and predators (for those with less resistant seeds) (Beaune *et al.* 2013b, Gautier-Hion *et al.* 1985). The red duikers spit out hard seeds (e.g. *Antrocaryon klaineanum*) during rumination (Gautier-Hion *et al.* 1985), but the seed size and the weak coat resistance of *D. normandii* suggests a vulnerability to crushing and destruction during mastication (as with *Santira trimera*, Feer 1995b, Gautier-Hion *et al.* 1985).

CONCLUSIONS AND PERSPECTIVES

This study identified six taxa as dispersers of *Dacryodes normandii* seeds and eight as seed predators, out of 14 vertebrate taxa observed consuming the fruits. As some frugivores may fulfil multiple roles, complementary and specific studies (faecal analysis and germination experiments, seed displacement monitoring, identification and germination trials of seeds in rodents' burrows, rumen and stomach content characterization, etc.) are required to contribute to a fuller understanding of the extent of seed predation and dispersal of *D. normandii*.

The main dispersers identified in this study are great apes: the western lowland gorilla (*Gorilla gorilla gorilla*) and, to a lesser extent, the central chimpanzee (*Pan troglodytes troglodytes*). African great apes are known to disperse the seeds of many species some of which provide timber and non-timber forest products (this study, Doucet 2003, Fourrier 2013, Petre *et al*. 2015, Tutin & Fernandez 1993, Williamson *et al.* 1990) or are endemic to the Gabonese forests (this study, Tutin *et al.* 1991). In particular, the western lowland gorilla is thought to provide incomparable dispersal services because of seed dispersal directed to open-canopy habitats (Petre *et al.* 2013, Rogers *et al.* 1998, Voysey *et al.* 1999).

Gorillas and chimpanzees are endangered; threatened by habitat loss and modification, epidemic diseases (such as Ebola haemorrhagic fever), commercial hunting (for bushmeat, the pet market and trophies) and persecution as a result of human–wildlife conflicts (Walsh *et al.* 2008). The depletion of great apes would result in changes in seed dispersal and seedling recruitment which would in turn impact upon forest ecosystem dynamics and regeneration (Effiom *et al.* 2013, Petre *et al.* 2013, Wright *et al.* 2000).

Therefore, this study encourages the implementation of great ape conservation strategies as critical to ensuring the preservation of tropical forest ecosystems. The maintenance of great ape dispersal services may also participate in the sustainable management of timber and non-timber forest product species.

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Appendix 1. Results of excavation of rodent burrows in the search for *Dacryodes normandii* seeds in a Gabonese logging concession

Species	Family	Occurrence	Total number of seeds
Antrocaryon klaineanum Pierre	Anacardiaceae	1	1
Canarium schweinfurthii Engl.	Burseraceae	2	2
Dacryodes buettneri (Engl.) H.J. Lam.	Burseraceae	2	10
Diogoa zenkeri (Engl.) Exell & Mendonça	Olacaceae	2	3
Elaeis guineensis Jacq.	Arecaceae	1	1
Olacaceae spp.	Olacaceae	12	119
Panda oleosa Pierre	Pandaceae	1	30
Pseudospondias microcarpa (A.Rich.) Engl.	Anacardiaceae	1	15
Santiria trimera (Oliv.) Aubrév.	Burseraceae	2	2
Undetermined	Undetermined	1	11
Empty burrows		15	
Total		40	194