AN INVESTIGATION OF FACTORS INFLUENCING THE GRAZING OF RAGWORT (*Senecio jacobaea* L.) BY SHEEP (*Ovis aries* L.) ON A HILL COUNTRY FARM

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Abstract

Grazing by sheep (*Ovis aries*) can control ragwort (*Senecio jacobaea*), but some flock members seldom eat it. For mature ewes, 11% appeared to avoid eating ragwort, compared with 16% of hoggets and 25% of lambs. Reluctant and avid ragwort feeders from each age group were fed ragwort indoors. During 5-min feeding sessions on three consecutive days, sheep classed as ragwort-averse, regardless of age, consumed less ragwort than avid ragwort eaters. Half of the ragwort-averse and avid ragwort eaters were confined on ragwort containing pasture for 10 days. Avid eaters consumed 45% of the volume of tagged ragwort plants within two days compared with no ragwort grazing by averse sheep. After 10 days, the ragwort-averse sheep consumed a similar rosette volume as the avid eaters, but lower volumes of elongated plants. Scan-sampling before and after confinement detected no change in the ragwort grazing of avid and averse sheep. Two further days of indoor ragwort grazing detected no differences in the behaviour of sheep that experienced restricted grazing compared with those that did not. The ragwort grazing of ragwort-averse and avid ragwort eaters may not be modified easily. The effects of pre-weaning ragwort exposure and post-weaning grazing with ewes on ragwort grazing by lambs were studied. Sampling periods were Weeks 1, 3, and 12 following weaning. Grazing behaviour was observed for 1-hour daily and the 24-hour reduction in ragwort volume measured on each of 4 or 5 consecutive days. Lambs exposed to ragwort before weaning consumed more ragwort than non-exposed lambs during the first two sampling periods. Lambs from ragwort-free pasture that grazed with ewes spent more time grazing ragwort than lambs grazing alone from the same background during Weeks 1 and 3. These effects did not persist into the 12th week following weaning. Lambs in all groups increased their ragwort eating markedly between Weeks 3 and 12. This may indicate an increased ability of lambs to consume ragwort with increasing age or an acclimation period in which all lambs come to accept ragwort. Grazing management techniques employed before, and immediately after weaning, appear not to effect the long-term ragwort eating of lambs.

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Chapter One

Introduction and Literature Review

Ragwort (*Senecio jacobaea* L.) is a weed of cattle pasture found in New Zealand, North Western areas of the United States, Europe, and elsewhere (Wardle, 1987). Cattle and horses tend to avoid grazing ragwort which contains pyrrolizidine alkaloids that are highly toxic to them (Cheeke, 1994). Despite this natural avoidance, accidental or forced ingestion can occur, and stock losses often result (Sharrow and Mosher, 1982). Grazing by sheep is an effective ragwort-control method (Poole and Cairns, 1940; Sharrow and Mosher, 1982; Amor *et al.*, 1983; Betteridge *et al.*, 1994). Unlike cattle, sheep can tolerate, and often readily include, large amounts (up to 50%) of ragwort in their diet (Cheeke, 1994).

In New Zealand, a trend towards all-cattle farming has seen the subsequent removal of sheep from previously integrated sheep and cattle systems. This has resulted in dense stands of ragwort in areas where previously it was not a problem (Betteridge *et al.*, 1994). Re-introducing a minimum number of sheep to control ragwort infestations could be a suitable compromise (Betteridge *et al.*, 1994). However, quantifying the minimum number of sheep relies on all individuals having similar ragwort-eating behaviour. In practice this appears not to be the case and a small proportion of sheep may avoid eating ragwort altogether (Betteridge *et al.*, 1994). The relative incidence of these sheep and factors that influence the grazing of ragwort by them, is the focus of this study.

Several excellent reviews describe the ecology and management of ragwort, *Senecio jacobaea* L. (eg. Atkinson, 1926; Cameron, 1935; Poole and Cairns, 1940; Harper and Wood, 1957; Harper, 1958; Wardle, 1987; Watt, 1987b; Bain, 1991; Beskow, 1995). To avoid redundancy the following review will focus mainly on factors pertinent to ragwort's success as a weed, with emphasis on how to control its spread.

1.1. Ragwort biology

1.1.1. ***History and distribution*** Ragwort is a herbaceous, broadleaved member of the plant family Asteraceae and is native to Europe and Asia (Wardle, 1987). It is now established in many temperate regions including Africa, the United States, Canada, Australia, and New Zealand (Mitich, 1995).

The word "ragwort" entered the English language in 1450, and is thought to refer to the ragged appearance of the indented leaves of the ragwort plant (Simpson and Weiner, 1989). In Britain *Senecio jacobaea* is usually called "common ragwort" to separate it from other *Senecio* species, although other names, including stavewort, kettle-dock and felonweed, are still used in various localities (Mitich, 1995). "Stinking willy" was once widely used as a name for the plant in the United States (Bain, 1991) before "tansy ragwort" became the present norm.

Ragwort has been present in New Zealand since at least 1874, when it was reported as growing near Dunedin (Thomson, 1922). Declared a noxious weed in 1900 (Poole & Cairns, 1940), it has spread over the North, South, Chatham, and Kermadec Islands (Webb *et al.*, 1988) - wherever growing conditions permit (refer to section 1.1.4.).

1.1.2. ***Description*** During development ragwort shows three separate growth forms, classed as seedlings, rosettes, or elongated flowering plants (Beskow, 1995).

The first above ground signs that a ragwort seed has germinated are the two cotyledons which emerge as seed leaves (Poole and Cairns, 1940). After a month, the seedling produces its first true leaf which is ovate (egg-shaped) with an undulate margin (Harper, 1958). Successive leaves are increasingly pinnatifid, and the segments produced by this indentation are themselves ragged and strongly overlapping (Atkinson, 1926). Leaf colour varies between plants and ranges from light to dark green (Bedell *et al.*, 1981), although the undersides of leaves are generally lighter than the upper surfaces (Beskow, 1995). Once the seedling produces more than 4 or 5 fully expanded true leaves it is called a rosette (Beskow, 1995).

Transition from a seedling to a rosette is also marked by the gradual replacement of the initial tap root by a thick rootstock with numerous white, fleshy, adventitious roots (Poole and Cairns, 1940). These roots grow horizontally at 10-12cm below the soil surface and beneath the main zone of grass roots (Harper, 1958). Rosettes may grow to a diameter of 40cm (**Plate 1**) before the stem elongation associated with flower production begins (Poole and Cairns, 1940). The stalked leaves of the rosette (root leaves) are usually shed before flowering begins and the leaves produced by the elongating stem are stalkless and joined directly to it (Harper and Wood, 1957).

The surfaces of some elongated plants are very smooth whilst others have cottony hairs, especially under the leaves and where the leaves join the stem (Atkinson, 1926). The single stems of undamaged flowering plants branch above the middle (**Plate 2**) and form flat-topped clusters of flower heads, called 'corymbs' (Poole and Cairns, 1940). The individual flower heads (capitula) measure 2cm in diameter, are bright yellow in colour, and possess 10-15 spreading rays, with each ray connected to one of the outermost florets (flower units that produce one seed each) of each capitulum (Atkinson, 1926). These 'ray' florets form a border around approximately 4.5 times as many 'disc' florets (Harper and Wood, 1957).

The seeds (achenes) derived from the disc florets are covered with fine hairs and are lighter than the hairless ray floret achenes (Watt, 1993). A further difference between the two types of seed is that disc achenes retain a group of long hairs (pappus), shed by ray achenes, that appear to aid dispersal by wind (McEvoy, 1984).

Ragwort plants commonly have 70-2500 capitula forming the inflorescence, with each capitulum producing an average of 70 seeds (Cameron, 1935). Up to 90% of the seeds are viable (Popay and Thompson, 1981). Mature flowering plants can reach a height of 1.75 metres under ideal growing conditions (Poole and Cairns, 1940).

1.1.3. ***Propagation*** The life cycle of ragwort is usually that of a biennial; it flowers, seeds and dies between 12 and 24 months after germinating (Popay and Thompson, 1981). Plants subjected to intense and/or frequent damage (such as trampling and grazing by stock) tend to act as weak perennials, taking more than two years to flower (Bedell *et al.*, 1981). To further confuse matters, a small percentage of ragwort plants can also act as annuals; completing their life cycle within a single year when conditions are particularly favourable (Schmidl, 1972).

Although seed production is the main method of ragwort propagation, vegetative reproduction can also occur, and usually involves the formation of plants with multiple crowns (growing regions) that produce many flowering stems (Poole and Cairns, 1940). These stems, usually formed as a result of plant damage, eventually become separate plants when the original crown rots away (Wardle, 1987). Schmidl (1972) reported that 35% of undamaged ragwort plants also form multiple crowns; suggesting that damage is not necessarily a prerequisite for vegetative propagation. A second method of vegetative propagation by ragwort occurs when individual fragments of severed roots grow into separate new plants (Poole and Cairns, 1940).

Plate 1. Large ragwort rosette.

Plate 2. Elongated ragwort plant with large yellow corymbs.

1.1.4. ***Habitat and dispersal*** Ragwort is generally regarded as a coloniser of bare or disturbed ground and is not well adapted for invading continuous, established grassland swards (Cameron, 1935; Harper, 1958). It is often found growing on badly managed pasture where gaps in the turf have occurred through either overgrazing, drought, stock-treading, and/or rabbit infestation (Watt, 1987b). A further source of suitable pasture gaps for ragwort establishment are those produced when mature ragwort plants die after seeding (McEvoy, 1984). Ragwort is also an integral component in the natural development of some British sand-dunes (Watt, 1987b). In New Zealand, ragwort was often a feature of partially cleared land, where tardiness in the removal of logs and stumps delayed pasture development or crop cultivation (Cameron, 1935).

Ragwort grows well in areas of relatively high rainfall and where precipitation occurs during most months of the year (Bain, 1991). In New Zealand, ragwort thrives where the annual rainfall exceeds 890 mm (Poole and Cairns, 1940). The worst ragwort infestations in Victoria, Australia, occur in areas that receive 760 - 1900 mm of rain annually (Schmidl, 1972). Medium to light, well drained soils, such as grey sands, grey loams or light rhyolite, provide the best substrate for ragwort growth (Poole and Cairns, 1940), although it does colonise many different soil types (Bain, 1991). Ragwort is usually absent from strongly leached soils, or those with a pH outside the range of 3.95-8.2 (Harper and Wood, 1957).

In New Zealand the shedding of seeds by ragwort begins in late December, with the largest releases occurring during March and April (Poole and Cairns, 1940). The three main vectors involved in the dispersal of ragwort seed are wind, water, and animals, including humans (Harper and Wood, 1957; Bedell *et al.*, 1981). The hairy, parachute-like pappus of the disc achene appears to help the seeds traverse long distances propelled by the wind (Cameron, 1935). However, research by Poole and Cairns (1940) suggests that most ragwort seed does not fall more than 10 m away from the parent plant, although a prevailing wind can propel a very small number (<1%) at least 36.6 metres. Rain and humid conditions can cause the pappus to become matted, rendering it ineffective as a dispersal mechanism (Harper and Wood, 1957).

Poole and Cairns (1940) suggest that flowing waterways could carry seeds to new establishment sites downstream, and that Waipa river and South Karori stream are possible examples of where this occurs. Ragwort seeds germinate quickly in fresh water; so fast flowing waterways would probably be the most effective at dispersing them over large distances before seedling death occurs as a result of germination without access to soil (Poole and Cairns, 1940).

Humans are probably the most effective agent of long-distance ragwort dispersal. The movement of ships with ragwort present in the ballast is probably responsible for much of its spread along the eastern North American coastline (Bain, 1991). Railway and road construction also provides long tracts of disturbed earth for ragwort to colonise and disperse along (Harper, 1958). The transportation of hay-bales containing seeding ragwort plants is a major cause of ragwort spread from Oregon and Washington to more eastern areas of the USA (Bedell *et al.*, 1981). In New Zealand railway development played an important role in the early dispersal of ragwort (Black, 1922). Further, ragwort seeds were often present as an impurity in nationally distributed sacks of imported grass and clover seed (Atkinson, 1926; Poole and Cairns, 1940), although this is less of a problem today (Radcliffe, 1969).

Birds and grazing mammals probably contribute a great deal to ragwort dispersal, although little research exists in this area (Wardle, 1987).
Collinge (1913; cited in Harper, 1958) and Salisbury (1961) have both reported the incidence of viable ragwort seeds in bird droppings: a bull-finch in the case of Collinge. However, intact ragwort seeds do not pass through the digestive tracts of zebra finches and sparrows (Poole and Cairns, 1940), suggesting that only some bird species can disperse them successfully. This species specificity does not apply to the external transportation of ragwort seeds entangled in bird's feathers; proposed by Poole and Cairns (1940) as a possible dispersal route. Birds can also disperse seeds attached to their feet with mud (Salisbury, 1961), although there is no record of this happening with ragwort seed.

Like birds, grazing mammals have the potential to disperse ragwort seeds that become attached to their bodies (Salisbury, 1961). Both cattle and horses have emerged from bad ragwort infestations with their coats covered in seed (Poole and Cairns, 1940), and Schmidl (1972) suggests that seed dispersal occurs when it is present in mud affixed to hooves. The proliferation of ragwort along roadsides used for stock movements is probably evidence of ragwort dispersal by farm animals (Poole and Cairns, 1940), although this correlation has never been studied experimentally (Wardle, 1987). One well-researched mode of ragwort dispersal by stock is the ability of sheep to pass viable ragwort seeds through their digestive tract, with subsequent germination occurring in the expelled droppings (Eadie and Robinson, 1953). Guthrie-Smith (1953) thought that horses were responsible for the spread of ragwort on a New Zealand sheep station, and assumed that they had ingested ragwort seed because most of the seedlings grew from horse droppings. However, horses rarely eat ragwort (Atkinson, 1926), and a second possibility is that seeds attached to the coat and hooves of the horses fell to earth and germinated in the only available gaps in the pasture sward; those provided by the droppings. Watt (1987a) found that ragwort established extremely well when scattered on ex-cow-dung patches compared with the surrounding pasture. In Hampshire's New Forest, ragwort is common only in the latrine areas of ponies, cattle, and deer (Edwards and Hollis, 1982).

1.2. Ragwort as a weed

A weed can be defined as "a plant growing where it is not desired" (Carter, 1990). The perception of a plant as a weed is therefore a matter of personal opinion; based on factors including purely aesthetic considerations, perceived medicinal or other practical properties, and whether the presence of the plant results in economic loss. In the case of ragwort, herbalists may perceive it as useful for dying cloth yellow (Hoffmann, 1987), whereas a dairy farmer might consider it a poisonous plant inhabiting valuable pasture space (Poole and Cairns, 1940). In a survey of predominantly North Island dairy farmers conducted by Bourdôt *et al.* (1994), 77% of the 147 respondents independently labelled ragwort as being a problem weed on dairy farms. This made ragwort infestation the most common weed problem listed by dairy farmers, who also rated the need for ragwort research higher in priority than for any other weed species. These statistics are not surprising because ragwort thrives on cattle-only farms and its ingestion is the leading cause of livestock poisoning by plants in both New Zealand (Mortimer and White, 1975) and Britain (Mayer, 1990).

1.2.1. *Toxicity* Alkaloids are cyclic, naturally occurring, nitrogenous plant compounds, and many are physiologically active when ingested by animals (Molyneux and Ralphs, 1992). There are many different types of plant alkaloids, and well-known examples include cocaine, morphine and nicotine (Brown, 1987).

A variety of plant species within genera such as *Heliotropium*, *Echium*, and *Senecio* contain pyrrolizidine alkaloids (Johnson *et al.*, 1989). Pyrrolizidine alkaloids (PAs) are the esters of necine ring structures (Wachenheim *et al.*, 1992), and over 100 have been identified and structurally mapped (Deinzer *et al.*, 1977). PAs can differ in the type and number of both the ester and ring elements of their construction (Wachenheim *et al.*, 1992). For example heliotrine, found in species of the genus *Heliotropium*, has only a single ester (Wachenheim *et al.*, 1992), whereas the PAs of the genus *Senecio* all have 2 in the form of large cyclic diesters (lactones) of the 1,2-dehydropyrrolizidine ring system (Deinzer *et al.*, 1977). In addition to structural differences, there is considerable variability in the toxicity of the pyrrolizidine alkaloids found in *Senecio* species, and a minority are not toxic at all (Johnson *et al.*, 1989). Mortimer and White (1975), suggest that the presence of a single double bond in the ring structure of a pyrrolizidine alkaloid may be a good indicator of its potential toxicity; with those that possess it being more toxic than those that do not. Ragwort has 9 pyrrolizidine alkaloids and all of them have rings with single double bonds (Molyneux and Ralphs, 1992). These PAs constitute around 0.3% of the dry weight of ragwort (Johnson *et al.*, 1989) and include senecionine, seneciphylline, jacoline, jacobine, jaconine, and jacozine (Deinzer *et al.*, 1977). All parts of ragwort plants, except the stems, contain toxic levels of PAs, although greater concentrations occur in the flowers than in the leaves (Bedell *et al.*, 1981). The overall PA content of ragwort also varies within seasons and between years (Johnson *et al.*, 1989).

Pyrrolizidine alkaloids in plants probably evolved as a protective measure against insect attack, and their toxicity to livestock may be purely coincidental (Molyneux and Ralphs, 1992). Ironically, PAs are non-toxic to mammals in their ingested form (Bedell *et al.*, 1981), and it is only after oxidation in the liver by multifunction oxidases (MFOs) that they convert to hepatotoxic pyrrole derivatives (Molyneux and Ralphs, 1992). These pyrroles cross-link with DNA and prevent the natural replacement of dead liver cells by inhibiting cell mitosis (Mayer, 1990). This interruption of liver cell function is cumulative, and successive sub-lethal doses of PAs eventually causes liver failure and the death of the animal (Johnson *et al.*, 1989). PAs can also destroy animal tissues directly (necrosis) or induce blood vessel swelling (oedema) or vascular disease (Hooper, 1978).

The external symptoms of pyrrolizidine alkaloid poisoning displayed by cattle include abdominal pain, constipation, rectum prolapse, weight-loss, and partial blindness (Ellison, 1994). Horses exhibit similar symptoms, as well as numerous behavioural disorders, such as restless pacing and "head-pressing" (Mayer, 1990). With sheep, jaundice is a common symptom (Mortimer and White, 1975), with affected flocks being described as 'yellow sheep' (Atkinson, 1926). Unfortunately, the observable symptoms of ragwort poisoning are common to many animal ailments and this can make it difficult to correctly diagnose the problem (Ellison, 1994). Also, the progressive nature of the liver disease induced by recurrent sub-lethal doses of ragwort means that an animal may not display symptoms of poisoning for up to 18 months after first ingesting it (Johnson, *et al.*, 1989). This delay can lead to ragwort being overlooked as the source of poisoning - especially if the animal has had no recent exposure to it (Mortimer and White, 1975).

Long intervals between ingestion and eventual poisoning by ragwort were probably responsible for ragwort remaining unconfirmed or unrecognised as the cause of several livestock diseases until the early 1900s (Atkinson, 1926). These diseases included 'stomach staggers' of horses in England and Wales, 'Pictou disease' of cattle in Nova Scotia, and 'Sirasyke' in Norway (Cameron, 1935). In New Zealand the disease took its name (Winton Disease) from the Winton district of Southland, where many horses and cattle died from liver cirrhosis after ragwort became established there around 1880 (Thomson, 1922). The ragwort then dispersed along railway lines to adjacent towns and the mysterious disease appeared to spread with it (Black, 1922). A further outbreak of Winton disease occurred in 1901 on a ragwort infested property in Auckland (Atkinson, 1926; Black, 1922). This led to renewed research efforts into its cause, and in 1902 New Zealand veterinary officers were the first to confirm the relationship between ragwort and the disease worldwide (Atkinson, 1926).

Another factor that obscured the relationship between ragwort and Winton disease is that farmers rarely observed the consumption of ragwort by cattle and horses (Atkinson, 1926). This is because horses and cattle usually avoid grazing ragwort in pasture where both grasses and ragwort are abundant

(Bedell *et al.*, 1981). It is only after the depletion of preferred species through either overgrazing or periods of drought that ragwort may become acceptable to stock (Harper and Wood, 1957). Once cattle have been 'forced' onto ragwort, some individuals may develop a fatal preference for the plant (Harper, 1958) or sometimes, just the flower heads (Molyneux and Ralphs, 1992).

Most stock poisoning from ragwort occurs after the consumption of contaminated hay or silage, because animals are unable to exercise their usual selectivity when eating processed feed (Bedell *et al.*, 1981). Ragwort also becomes more palatable to stock when wilted or dried, but it does not decrease in toxicity (Popay and Thompson, 1981). To illustrate the poisoning potential of contaminated feed Watt (1987b) described a case history where one third of 270 weaned calves died after 11-12 weeks of consuming silage with a 1% ragwort component. Human poisoning can also occur from 'disguised' ragwort material present in contaminated cereals, herbal teas, and milk products (Johnson, *et al.*, 1989). Honey produced from ragwort nectar is also toxic, however it is usually too 'off-coloured' and bitter to market (Deinzer *et al.*, 1977; Thomson, 1922). Milk products become contaminated following the ingestion of ragwort by lactating animals (Johnson, *et al.*, 1989).

Animal species differ greatly in their susceptibility to pyrrolizidine alkaloid poisoning (Hooper, 1978). Cattle and horses, for example, are especially vulnerable, whereas sheep are up to 75 times more resistant (Cheeke, 1984). The sensitivity of selected species to the PAs in ragwort are summarised in **Table 1.1.**. Estimates of lethal ragwort doses are commonly expressed as a proportion of body weight (**Table 1.1.**). However these estimates are oversimplified because toxicity also depends on rates of plant ingestion and specific alkaloid concentrations within the plant (Johnson, *et al.*, 1989).

Cheeke (1994) suggests that the differences between species in PA sensitivity result from divergent feeding strategies that have left grazers (eg cattle, horses) well adapted to diets of non toxic grasses but intolerant to the chemically-defended herbaceous plants with which forb grazers (eg sheep) co-evolved. Browsers have evolved PA detoxification systems that grazers lack, although the exact mechanisms are unresolved (Cheeke, 1994). For example, the site of PA detoxification in sheep is a point of contention, with both the liver and the rumen suggested as likely possibilities (Cheeke, 1994; Wachenheim *et al.*, 1992).

Table 1.1. Comparative sensitivity of various animal species to dietary *Senecio jacobaea* (Cheeke, 1994).

Species	Chronic Lethal Dose of Ragwort (% body weight)
Gerbil	3640
Japanese quail	2450
Guinea pig	525
Hamster	340
Sheep	300
Goat	125
Rabbit	115
Rat	20
Horse	7
Cow	4

Cattle create pyrrols
∴ don't detoxify pyrrols.

Compared to cattle, sheep have proportionately less of the liver enzymes that bioactivate PAs into highly toxic pyrroles, as well as higher levels of PA detoxifying enzymes, such as epoxide hydrolase (Cheeke, 1994). In contrast, detoxification in the rumen probably occurs through the activities of PA-biotransforming bacteria that form 0.3% of the rumen bacterial populations of sheep compared with only 0.1% in cattle (Wachenheim *et al.*, 1992). Recent experiments (Anon, 1997) have shown that the transfer of PA-biotransforming bacteria from a sheep to a cow's rumen can protect the cow from PA toxicosis. This finding suggests that the rumen plays an important role in PA detoxification in sheep, although it does not eliminate the possibility of the liver functioning as a concurrent site. Resistant herbivores, such as guinea pigs, that do not possess a rumen probably rely on the liver for PA detoxification, although the mouth, buccal cavity and digestive tract lining may also contain essential biotransformation enzymes (Cheeke, 1994).

1.2.2. *Relative forage reduction* Once established, ragwort plants can out-compete most other pasture species, with the exception of tall hay crops (Harper, 1958). Popay and Thompson (1981) suggested that a smothering effect caused by ragwort plants could reduce overall pasture production, however, Wardle *et al.* (1995) found no evidence of this proposed inhibition, and instead found that increased production often occurs. This observed facilitation of some pasture species growing beneath ragwort probably results from an improved microclimate and less stock trampling (Wardle *et al.*, 1995). Regardless of whether ragwort enhances pasture production, under-utilisation of the available pasture by cattle is inevitable when ragwort is present (Popay and Thompson, 1981; Wardle *et al.*, 1995). This is because cattle avoid ingesting ragwort by not grazing in the immediate vicinity of ragwort plants, which leaves nearby pasture also untouched (Popay and Thompson, 1981).

1.3. Ragwort control

The decision to try to control any weed depends upon the likely benefits of doing so weighed against the probable costs; 'no control' is sometimes the cheapest option (Popay and Field, 1996). With ragwort, weed control legislation often makes this type of cost/benefit analysis redundant (Bourdôt *et al.*, 1994; Popay and Field, 1996). For example, the New Zealand Noxious Plant Act requires that ragwort be controlled within 20 m of all farm boundaries.

The old adage "prevention is better than cure" definitely applies to the economics of ragwort control (Bedell *et al.*, 1981). However, preventing an initial ragwort infestation, or the re-establishment of ragwort after the implementation of a control program, can require extensive revision of conventional management practices that promote its growth and spread (Burrill *et al.*, 1994). This usually involves implementing procedures that promote an actively growing, continuous sward of desired plant species that ragwort cannot easily invade (Cameron, 1935; Wardle, 1987). In farming situations continuous swards are difficult to maintain and the persistence of ragwort in the face of even the most rigorous management regimes suggests that containment is a more realistic control objective than complete eradication (Popay and Field, 1996).

There are a variety of ragwort control methods; used either individually, or in combination (Bedell, *et al.*, 1981). Deciding between them involves considering of a variety of factors, including cost, effectiveness, speed of action, and permanence of control (Poole and Cairns, 1940). The relative importance of these considerations will depend on issues such as the size, growth-stage and location of the infestation (Poole and Cairns, 1940; Bedell, *et al.*, 1981). For example, to satisfy legal requirements, a method that immediately removes all evidence of a clearly visible ragwort infestation may prevent the implementation of a less aesthetic, but more permanent long-term program of similar cost.

1.3.1. ***Life-cycle completion*** Of all the methods available for ragwort control, life-cycle completion, also called Matthews technique, is the cheapest and simplest. It involves allowing mature (especially multi-crowned) ragwort plants to set seed and die, leaving only the more easily controlled vegetative rosettes as a problem (Popay and Thompson, 1981). Drawbacks with this method are that it increases the ragwort seed bank (Wardle, 1987) and around 10% of plants regenerate after flowering (Thompson, 1985). Unfortunately, it is illegal to allow ragwort to flower and set seed in New Zealand, so using Matthews technique requires co-operation from a Noxious Plant Officer (Popay and Thompson, 1981).

1.3.2. ***Hand pulling and grubbing*** For small, isolated ragwort infestations, removing plants by hand is often the most economical control option (Bedell *et al.*, 1981). It is important to remove as much of the root system as possible, because fragments left in the soil can regrow (Popay and Thompson, 1981). For this reason, hand pulling is preferable to grubbing because it severs fewer roots during plant removal (Poole and Cairns, 1940). Elongated ragwort plants are much easier to pull out than rosettes, especially if the ground is damp, and more of the root comes out with them (Harper, 1958). Hand-pulling can become a habitual exercise practiced during other farm operations, and kills 66% of elongated plants (Poole and Cairns, 1940). Because pulling works best when plants are almost flowering, it is important to destroy plants immediately after removal to prevent them seeding (Popay and Thompson, 1981). Burning is an effective disposal method (Atkinson, 1926).

1.3.3. ***Flame-throwers.*** Poole and Cairns (1940) found that after "thoroughly scorching" seeding ragwort with a flame-thrower none of the burnt seeds remain viable and only 7% of plants regenerate. Spot-treating flowering ragwort plants with a flame-thrower is quite labour intensive and probably only suitable for mild infestations (Poole and Cairns, 1940). Flame-throwers can be hazardous when used during high fire risk months.

1.3.4. ***Mowing*** Cutting elongated ragwort plants prevents flowering and makes the pasture look tidy (Popay and Field, 1996). However, instead of killing the plant, mowing damage encourages the growth of multiple stems and vigorous flowering in later seasons (Poole and Cairns, 1940). Mowing is also ineffective if cut plants release seed or poison grazing animals after being left on the ground rather than destroyed (Burrill *et al.*, 1994). Cattle are more likely to eat ragwort that has wilted after being cut (Harper, 1958). Ragwort infestations typically contain plants at all stages of the life cycle, and although a single mowing will prevent seeding by the plants flowering at cutting time, it will not effect plants that elongate later in the season (Bedell *et al.*, 1981). Therefore, to reduce ragwort infestations, mowing must be thorough and frequent (Harper, 1958). Mowing can be physically impossible in areas such as steep, remote hill country (Schmidl, 1972).

1.3.5. ***Pasture renovation.*** Of the mechanical methods available for ragwort control, pasture renovation is the most extreme. It usually involves ploughing the infested pasture to enable the development of a more competitive sward the following year (Harper, 1958). In the interim, growing a crop or leaving the land fallow are management options, although timely ploughing to destroy any ragwort seedlings before sowing the new pasture is important (Bedell *et al.*, 1981). Pasture renovation is an expensive control option and, like mowing, may be physically impossible in some situations (Beskow, 1995).

1.3.6. ***Chemical herbicides*** Because humans subjectively categorise vegetation as either plants or weeds, there is often the naive expectation that herbicides will make the same distinctions. In reality this rarely happens, and the most popular ragwort herbicides (eg 2,4-D, picloram and dicamba) also damage clovers (Popay and Thompson, 1981). Depending on the soil persistence of the herbicide, it can take from 4 months (2,4-D) to 2 years (dicamba and picloram) for the original clover balance to return (Popay, 1981). Thus herbicide use in pasture, although reducing the risk of animal poisoning from ragwort, can result in lower animal production than untreated pasture because of a decline in clover content (Beskow, 1995).

Of the available clover-safe herbicides, asulam provides just 90% ragwort control (Forbes, 1982); Flazasulfuron damages perennial ryegrass (James *et al.*, 1997); and 2,4-DB is only useful for controlling seedlings (Popay and Thompson, 1981) because ragwort, like most weed species, is more resistant to herbicides during the later stages of its life cycle (Wardle, 1987). Applying greater rates of herbicide, such as 2,4-D (but not 2,4-DB) when treating large rosettes or flowering plants, can help overcome the problem of older plant resistance (Popay and Thompson, 1981), however it increases the cost of control and generates greater clover damage unless carefully directed (Thompson and Saunders, 1984). Also, the practice of increasing herbicide application rates, especially 2,4-D, is becoming less acceptable in New Zealand, where an increase in horticulture has resulted in a trend toward reduced phenoxy herbicide usage (James *et al.*, 1997).

There are a variety of ways to apply herbicides, ranging from general broadcast methods to specific spot treatments (Popay, 1981). Broadcast spraying of large pasture areas is the simplest way to apply herbicides, and is used when damage to non-target species is either irrelevant, unanticipated, or expected to be minimal (Bedell *et al.*, 1981). In contrast, the spot treatment of specific plants, usually with a hand-held spray gun or rope-wick applicator, is much more labour intensive but often necessary to prevent non-target damage (Popay, 1981). To combat the mixed-age plants of established ragwort infestations whilst keeping clover damage to a minimum, the large plants are initially spot treated with clover-damaging picloram or dicamba followed by a broadcast spray of 2,4-D to control the seedlings (Popay and Thompson, 1981). Another spot treatment option for ragwort is the herbicide glyphosate, although incautious application can produce large gaps in the pasture because it kills all other pasture species (Rahman, 1993).

Although relatively quick and effortless to apply, herbicides do not instantly remove a ragwort problem (Bedell *et al.*, 1981). Treated plants die slowly, and remain poisonous to stock for 4 to 6 weeks after spraying (Burrill *et al.*, 1994). It is preferable to prevent stock from grazing the pastures during this dying off period because the toxicity of ragwort increases after herbicide application and it may become more palatable due to increased levels of water soluble carbohydrates (Popay and Thompson, 1981).

Herbicides only provide short-term solutions to ragwort problems if the management practices that facilitated the infestation remain unmodified (Bedell *et al.*, 1981). Ideally ragwort control methods should also improve the competitiveness of desired pasture species. A cost effective way to achieve this is to apply both herbicides and fertilisers (Nitrogen or Phosphorus) at the same time (Rahman *et al.*, 1993).

1.3.7. ***Biological control*** The natural enemies that restrict ragwort populations in Europe were usually absent from countries like New Zealand where accidental ragwort introductions occurred (Olson and Lacey, 1994). Although ragwort was not necessarily immune to herbivory by species native to these new countries, they usually had little effect on its spread (Cameron, 1935). One example is New Zealand's native magpie moth (*Nyctemera annulata*), the larvae of which feed heavily on ragwort without reducing infestations (Thomson, 1922). Thus, importing natural enemies usually forms the basis of ragwort biological control (Radtke, 1993).

Most of the biological agents recommended for ragwort control are insects (Bedell *et al.*, 1981). In New Zealand, three insect enemies of ragwort, cinnabar moth (*Tyria jacobaeae*), ragwort seedfly (*Pegohylemyia jacobaeae*), and ragwort flea beetle (*Longitarsus jacobaeae*), are now resident after being introduced expressly for ragwort control (Syrett *et al.*, 1984). They have the potential to reduce ragwort populations in hill country and other areas where the terrain is too rough and inaccessible to attempt mowing, plowing or chemical application (Bedell *et al.*, 1981).

Despite careful measures to introduce sufficient quantities of parasite-free biological control agents, many fail to establish as effectively as the target plant did (Cameron, 1935). Cinnabar moth became established only in the southern North Island of New Zealand, despite nationwide introductions made between 1926-31 (Syrett *et al.*, 1984). Similarly, the ragwort seedfly, first released in 1928, also has a poor establishment record and its central North Island range does not overlap with that of the cinnabar moth (Syrett *et al.*, 1984). In contrast, the ragwort flea beetle has established extremely well, enabling the translocation of beetles to fresh infestations from the original release sites (K. Betteridge, pers. comm.). The possibility of poor control agent establishment is an accepted risk associated with biological control programmes (Cameron, 1935).

Sometimes the actions of an imported natural enemy fail to control populations of the target weed (Cameron, 1935). For instance caterpillars of the cinnabar moth can cause extensive defoliation of ragwort, but the plant often survives to flower during the following year (Syrett *et al.*, 1984). However, the stress exerted on ragwort by such sub-lethal herbivory leaves it more susceptible to control by other species - such as the ragwort flea beetle (James *et al.*, 1992).

When it works, biological control is a cost-effective method of controlling ragwort. In Oregon, a ragwort biological control programme is credited with reducing livestock losses by US $3.7 million per annum, and every dollar invested provides an estimated return of 13 dollars in benefits (Radtke, 1993).

Biological control is a long-term ragwort control option because introduced insects can take several years to establish populations large enough to reduce weed infestations (Burrill *et al.*, 1994). This makes biological control more suitable for suppressing ragwort in ungrazed nature reserves and species-rich grasslands, rather than on farms where short term controls are the only sure way to prevent possible ragwort ingestion by stock (Bedell *et al.*, 1981).

1.3.8. ***Grazing control*** Ideally, weed control organisms should not cause damage to non-target species (Cameron, 1935), and some authors restrict their definition of biological control agents to those that display host-specificity (eg. Radtke, 1993). This means that the control organism should only eat or parasitise a single host (Cameron, 1935). Grazing animals, although often useful for controlling weed infestations, are usually generalist feeders that consume a wide variety of plant species (Popay and Field, 1996). However, unlike insect control agents, they can be fenced onto weed infestations at an intensity appropriate to the control of the target weed (Carter, 1990).

The availability of grazing animals is an important consideration when contemplating their usage in a weed control program, and in New Zealand cattle, goats and sheep are easy to obtain (Popay and Field, 1996). Attempts to control ragwort with grazing animals never involve cattle because of obvious toxicity problems (section 1.2.1.). Of the two remaining species, sheep are usually a better option than goats because they are easier to fence (Popay and Field, 1996) and more resistant to ragwort poisoning (Cheeke, 1994).

1.4. Using sheep to control ragwort

Compared to cattle, which are predominantly grass feeders, sheep actively select and consume large quantities of forbs (Hanley, 1982). This feeding strategy can make sheep ideal weed control agents because most noxious weeds are forbs (Olson and Lacey, 1994). Weeds successfully controlled by sheep include gorse seedlings (Popay and Field, 1996), spotted knapweed (Olson *et al.*, 1997), leafy spurge (Sedivec *et al.*, 1995), and ragwort (Sharrow and Mosher, 1982).

1.4.1. ***History and practices*** Using sheep to control ragwort is at least a 100 year old practice, with McAlpine and Wright (cited in Harper, 1958) recommending in 1894 that infestations be grazed with sheep during early summer. This grazing period exposes sheep to ragwort after many of the plants have flowered and may take advantage of an observed preference of sheep for young flower heads (Poole and Cairns, 1940; Eadie and Robinson, 1953). Other authors have maintained that sheep prefer to eat ragwort at the rosette stage and that the best time to graze infestations is during late winter to early spring when succulent rosettes are more palatable than dormant pasture species (Atkinson, 1926; Cameron, 1935).

Although sheep are resistant to poisoning by ragwort, mortalities may occur during extended confinement on heavily infested areas where grass is in short supply (Atkinson, 1926; Poole and Cairns, 1940). Restricting sheep grazing to times of the year when most ragwort plants are at the rosette stage reduces the risk of poisoning due to the relative absence of elongated plants with highly toxic flowers (Cameron, 1935). A second way to minimise poisoning is to alternate flocks between infected and clean pastures (Cameron, 1935; Poole and Cairns, 1940; Eadie and Robinson, 1953), although some infestations are too dense for grazing episodes to be effective (Atkinson, 1926). Some episodes may be harmful, such as moving sheep from ragwort infestations to clover-dominant pastures rich in copper (Coup, 1959). This is because the liver damage caused by ragwort prevents sheep from ridding themselves of excess copper, rendering them susceptible to fatal copper poisoning (Cheeke, 1988).

A simple way to avoid poisoning the sheep used in ragwort management programmes is to control only light or moderate infestations with them.

However, grazing by sheep may be the only economically viable option for quick regulation of severe ragwort infestations covering large areas (Poole and Cairns, 1940; Eadie and Robinson, 1953). In these situations using a "flying flock" to achieve control and then selling the fattened sheep before they succumb to ragwort poisoning is a recommended option (Coup, 1959). Harper (1958) suggested that sheep may fail to fatten readily on a ragwort diet, although a recent control study found that ewe hoggets reached a satisfactory 63 kilograms at 20 months old (Betteridge *et al.*, 1994). Also a nutritional analysis of ragwort showed that sheep could attain their dietary requirement from eating the leaves and flowers (Sharrow and Mosher, 1982).

Not on a ragwort diet!

The processed meat of sheep used for ragwort control is probably not a hazard to human health because it is only the damage caused by PAs that increases in animal tissues, and not the PAs themselves (Cheeke, 1988). A sacrifice flock may consist of either lambs (Mortimer and White, 1975) or ewes (Atkinson, 1926), although older sheep are more resistant to ragwort poisoning (Cameron, 1935). Older ewes also tend to be a more effective control because they graze the crown of ragwort plants (Atkinson, 1926), whereas younger sheep eat only the outer leaves (Cameron, 1935). — Not true!

1.4.2. ***Ragwort control with sheep on cattle-only farms*** The feeding practices of cattle tend to promote ragwort growth while those of sheep suppress it (Harper, 1958). In Victoria, Australia, Amor *et al* (1983) found that ragwort covered less ground area in pastures grazed by sheep (2%) than in pastures left ungrazed (5.5%), whereas cattle grazing increased the ragwort cover (11%). It is not surprising, then, that ragwort is frequently a problem on properties grazed only by cattle (Schmidl, 1972; Bourdôt *et al.*, 1994).

A common method used when attempting to control ragwort in cattle-only farming systems is to temporarily introduce sheep (Poole and Cairns, 1940). Sharrow and Mosher (1982) found that in pastures grazed only by cattle most ragwort plants die after setting seed. In contrast, a combination of cattle followed by sheep grazing allowed only 2% of ragwort plants to complete the life cycle, compared with 32% in the cattle-only treatment. There was no difference in the total mortality of ragwort plants between pastures grazed by cattle alone or with cattle followed by sheep, but more plants died as a result of grazing in the combined treatment (14% vs 2%). This suggests that grazing by sheep may reduce the ragwort seed bank over time, although the 1-year duration of Sharrow and Mosher's study was too short to explore this possibility (Wardle, 1987).

Sheep accomplish ragwort control by preventing plants from seeding (Bedell *et al.*, 1981). Long (1910) noted that "On land regularly stocked with sheep not a single ragwort can be seen". However, sheep grazing does not usually eradicate ragwort from pastures (Harper, 1958). Instead, it maintains a population of small rosettes; giving an appearance of elimination to the casual observer (Poole and Cairns, 1940). One concern is that these suppressed rosettes will flower following the replacement of sheep with cattle (Bedell *et al.*, 1981; Watt, 1993), although Sharrow and Mosher (1982) found that most of them die without setting seed. However, the potential of buried ragwort seeds to remain viable for up to 16 years (Thompson and Makepeace, 1983) suggests that a premature return to cattle-only grazing will encourage re-infestation from this source (Bedell *et al.*, 1981). Furthermore, ragwort infestations can fully recover within 2 years of removing sheep from them, even after 5-7 years of intensive grazing (Schmidl, 1972).

Once the temporary introduction of sheep has achieved acceptable ragwort control on a cattle-only farm, an accepted way to avoid reinfestation is to permanently retain some of the sheep (Atkinson, 1926; Cameron, 1935; Poole and Cairns, 1940). On cattle farms replacing some of the stock animals with sheep can increase the total meat production of the farm by 24% because the dietary habits of sheep and cattle differ (Walker, 1994). With dairy farming the presence of even a small flock of sheep can reduce milk production by almost 50%, although this may be an acceptable loss compared to the potential cost of replacing cows poisoned by unchecked ragwort infestations (Poole and Cairns, 1940).

The usual method of controlling ragwort with sheep is to apply appropriate grazing pressure by confining them to infested areas with fences (Cameron, 1935). However, many cattle and dairy farms lack sheep-proof fencing (Poole and Cairns, 1940). A second consideration is that cattle-only farms are often unequipped for shearing or handling sheep, although hardy, low maintenance breeds, like the fleece-shedding Wiltshire Horn, may be a suitable compromise (Harridine, 1987). Finally, a cattle farmer wishing to control ragwort with sheep must first determine the stocking rate needed to control the infestation as well as the best grazing strategy to employ (Betteridge *et al.*, 1994).

Possible grazing strategies include allowing sheep to graze with cattle (Watt, 1993), or to alternate sheep and cattle grazing (Poole and Cairns, 1940; Sharrow and Mosher, 1982). Allowing sheep to graze with cattle (set-stocking) appears to provide more reliable ragwort control than methods that require mob-stocking infestations with sheep at times when cattle are absent (Watt, 1993; Betteridge *et al.*, 1994). A further advantage of set-stocking is that sheep may become bonded to the cattle, lessening the need for sheep-proof fencing (Anderson *et al.*, 1994).

For dairy farmers, using the lowest possible number of set-stocked sheep to control a ragwort infestation will minimise the decrease in production caused by ragwort control. Betteridge *et al.* (1994) found that set-stocking ewe hoggets (one year old sheep) at a rate of 3 stock units per hectare (su/ha) provided better ragwort control than 1.5 su/ha. However, set-stocking sheep at rates of up to 4 su/ha may sometimes fail to control ragwort infestations (K. Betteridge, pers. comm.).

1.4.3. ***When attempts at sheep control fail*** Overgrazing by sheep on ragwort infested land, especially when the ground is dry, can exacerbate a ragwort problem by producing bare patches suitable for seedling establishment (Watt, 1993).

A second problem is that some sheep may not eat ragwort (Betteridge *et al.*, 1994). Poole and Cairns (1940) found that sheep from non-ragwort country would not eat ragwort until starved onto it, although some animals then developed a preference for the plant. Differences in grazing preferences between individual sheep are a common finding of grazing experiments (Walker *et al.*, 1992; Bell *et al.*, 1996). Betteridge *et al.* (1994) estimated that 5% of sheep from ragwort country may not eat ragwort. The reluctance of some sheep to eat ragwort could explain why attempts to quantify stocking rates for ragwort control have occasionally been unsuccessful.

From a ragwort control perspective, more information is needed about the relative incidence of ragwort-averse sheep. Being able to identify and remove these sheep from flocks intended for ragwort control may prevent the overgrazing of pasture. Developing simple training procedures that encourage preferential ragwort eating by ragwort-averse sheep would be beneficial.

The grazing experiences of lambs during weaning influence their food preferences as adult sheep (Ramos and Tennessen, 1992; Walker *et al.*, 1992). Grazing with mothers (Nolte *et al.*, 1990), older sheep (Chapple and Lynch, 1986), or conspecifics (Scott *et al.*, 1996), can also modify food preferences of lambs. Thus, exposing lambs to ragwort with their mothers before weaning may increase their consumption of it after weaning.

1.5. Aims

The objectives of this study were to determine:

(i) The proportion of sheep in a Romney flocks that rarely eat ragwort.

(ii) If a reluctance to eat ragwort differs between specific age/experience cohorts.

(iii) The robustness of any observed ragwort aversions.

(iv) The impact of different rearing conditions for Romney lambs on their subsequent ragwort grazing.

Chapter Two

The Incidence of Sheep that Rarely Eat Ragwort within Romney Flocks of Differing Age, and the Susceptibility of Ragwort Aversions to Behaviour Modification.

2.1. Introduction

A general assumption of ragwort management programmes that use grazing by sheep as a method of control, is that sheep readily eat ragwort (Atkinson, 1926; Cameron, 1935; Schmidl, 1972; Bedell *et al.*, 1981; Sharrow and Mosher, 1982). However, Poole and Cairns (1940) found that entire flocks of sheep obtained from ragwort-free farms initially avoided eating ragwort until all other pasture species became exhausted. Eadie and Robinson (1953) reported a similar finding in Australia, although they did not state whether the sheep were sourced from ragwort or non-ragwort country. The findings of Betteridge *et al.* (1994) suggest that even when sheep are reared from birth on ragwort infested pastures some animals may still avoid eating ragwort.

The possibility that some sheep eat less ragwort than others is disturbing because a farmer considering the purchase of sheep for ragwort control has no assurance that the procured animals will do the job intended. Developing a method by which farmers could quickly screen flocks to identify the best sheep for ragwort control would reduce the risk of buying ineffective animals.

Cameron (1935) suggested that ewes are better than lambs at controlling ragwort because they graze the crown of the plant and are less prone to poisoning. Animals susceptible to PA poisoning rarely graze plants that contain them (Cheeke, 1994). Therefore, if ragwort is more toxic to younger sheep than older ones, then perhaps the proportion of ragwort-averse individuals differs between flocks of different ages. Betteridge *et al.* (1994) found that 5% of hoggets (1 year-old lambs) appeared to avoid eating ragwort, but there is no information available for lambs or ewes. Determining the proportion of sheep of different ages that rarely eat ragwort could help farmers to make buying decisions in situations where different aged sheep are available for purchase.

For a farmer who already owns sheep that are reluctant to eat ragwort, a simple method for changing the eating behaviour of these sheep would be desirable. Poole and Cairns (1940) suggested that sheep initially averse to eating ragwort may eventually develop a preference for it after experiencing one or more occasions when ragwort was the only available forage. Two ways of providing these grazing conditions are (i) to allow confined sheep to deplete preferred pasture species until only ragwort remains (Poole and Cairns, 1940), or (ii) to place sheep in an artificial environment, such as an indoor pen, where ragwort is the only available food. The relative effectiveness of these two methods should be compared.

2.2. Objectives

To determine:

(1) The proportion of ragwort-averse sheep in Romney flocks.

(2) If a reluctance to eat ragwort differs between specific age/experience cohorts.

(3) To determine the robustness of any observed ragwort aversions after ragwort ingestion in both natural and artificial environments.

2.3. Methods and Materials

2.3.1. ***Study area*** The AgResearch "Ballantrae" Hill Country Research Station, previously used by Betteridge *et al.* (1994), was the site for the present study. The station is located 35 km east of Palmerston North on the Eastern side of the Ruahine ranges. As one of its operations, the research station has a 30 ha rotationally grazed bull beef finishing system in which ragwort is a major weed (Betteridge *et al.*, 1994). The sedimentary soils at Ballantrae are ideal for ragwort growth, as is the average rainfall of 1200 mm/year (A. Mackay, pers. comm.)

2.3.2. ***Identifying ragwort-averse sheep*** During the last week of February 1996, two flocks of sheep, one containing ewes (n=140) and the other hoggets (n=98), were the focus of a screening programme designed to identify both avid and reluctant ragwort eaters. The screening procedure involved 10 minute periods of *ad libitum* sampling of the ragwort feeding behaviour of 10 sheep at a time on ragwort infested pasture. The number of times each individual was observed eating ragwort during an observation period was recorded. To avoid fleece damage, each animal was initially identified by a colour combination of temporarily attached, spring-type clothes-pegs.

At the conclusion of screening, the 16 most avid ragwort eaters from each flock were labelled with a spraypainted dot on the head, and kept separate from their home flock. Sheep that had not been seen eating ragwort were also separated and retained for a second 30-min screening the following day. Only sheep displaying no obvious ragwort eating during the second screening were considered ragwort-averse. Sixteen of the ragwort-averse sheep from each flock were randomly selected for use in indoor feeding trials (Section 2.3.3) along with the two groups of 16 avid eaters.

A further two groups were selected from a flock of lambs (n=60) used in a previous experiment (Chapter 3). A detailed grazing history was available for each of the lambs, and this was used instead of screening to select both the ragwort-averse and avid ragwort eaters. The grazing data consisted of 120 instantaneous behaviour observations for each lamb. A lamb was classed as ragwort-averse if it had been observed eating ragwort on three or less occasions, and 14 lambs met this criterion. The 16 lambs observed eating ragwort on the greatest number of occasions formed the avid group. In total, 94 sheep in five groups of sixteen and one of fourteen were selected from the three different aged flocks, with one group from each flock classed as avid ragwort eaters and the other group as ragwort-averse.

2.3.3. ***Indoor presentation of ragwort to sheep*** In the first week of April 1996, all of the selected sheep (Section 2.3.2.) were confined indoors and presented with measured amounts of ragwort leaves. A purpose-built indoor feeding facility at Ballantrae was initially proposed as the venue for this ragwort acceptance study, however, a lack of yarding or drafting facilities and the large number of animals made this location impractical. Instead, a four-stand wool shed was chosen, because it had covered yards on both sides of the building. This allowed sheep to enter the shed from one side and exit on the other where they were penned until all the other sheep were tested. This meant that for each day the total time spent by the sheep in yards was the same for all animals. It also eliminated the possibility of testing the same individuals twice because tested and untested animals were never mixed.

In the two weeks before indoor presentations of ragwort began, all efforts were made to ensure that the sheep would actually eat while indoors. For the first four days the sheep were penned and herded through the wool shed without any food present, to habituate them to the surroundings. After this initial period, lush pasture cut with a lawnmower was provided in buckets placed in both the woolshed and the covered yards during periods when the sheep were being penned and herded. Finally, metal trays containing cut grass were presented to each sheep while penned for 5-mins inside the woolshed on each of five sequential days. All of the sheep ate cut grass indoors during this final pre-conditioning period, with the exception of one ewe classed as an avid ragwort eater. This ewe was not used for the ragwort presentation phase.

The first set of indoor presentations of ragwort began on 3 April 1996, and concluded on 5 April, with each sheep tested once on each of the three days. All the ragwort material used for indoor presentation was collected fresh each day, and the mean dry matter content determined. Only leaves were used, although these were obtained from both rosettes and elongated ragwort plants. Before testing began, the sheep were all drafted and penned according to their age and feeding class. The order that the six groups were tested was randomly determined for each day. The woolshed contained only enough pens to hold eight sheep at a time, so half of the animals from each group were tested followed immediately by the other half.

To begin testing, a metal tray with a measured amount (~200-gms) of fresh ragwort leaves was placed into a pen containing one sheep (**Plate 3**) and left for 5-mins. The tray was then removed and the remaining contents re-weighed, along with any ragwort material left on the floor of the pen. During each of the 5-min ragwort presentations, a tray containing ragwort was placed adjacent to the pens to measure any weight loss from water evaporation. Adjustments were made to the re-weighed material from grazed trays to include this wilting effect. The amount of ragwort consumed by the sheep was determined from the weight difference between the initial and remaining ragwort material. This value is also a rate of ragwort consumption, as long as all the material provided was not eaten by the sheep before the 5-min ragwort presentation finished.

Plate 3. Ewe eating ragwort from a metal tray during a 5-min confinement period indoors.

A further two days of indoor ragwort presentations were conducted on 29 and 30 April 1996 after half of the sheep in each group had spent 10 days confined on pasture with dense ragwort, while the other half enjoyed unrestricted grazing (Section 2.3.4.).

In both feeding trials, none of the sheep consumed all of the ragwort material during a 5-min presentation, and the average rate of ragwort consumption by the six groups was analysed using the GLM procedures of SAS (SAS Institute, 1990). The daily consumption rates for each animal were averaged before performing the analysis so that the sample size (n) was equal to the number of animals for each of the two sets of indoor trials (Martin and Bateson, 1986). The main effects of age, feeding category, week, and interim pasture type were tested, as well as the interactions between them.

2.3.4. ***Confining sheep on ragwort infested pasture*** On 10 April 1996, half of the sheep in each of the six age/feeding class groups were randomly allocated to confinement for 10 days on pasture densely populated with ragwort while the other half had unrestricted grazing. The averse and avid eaters allocated to the confinement treatment were formed into two mixed-age flocks and each was fenced onto a separate ragwort-infested pasture. The available dry matter per hectare of both pasture and ragwort for each confinement area was estimated by cutting and removing plant material from three randomly selected 1-m^2 areas and then weighing them before and after drying. The dry matter of the pasture remaining after 10 days of grazing in each confinement area was estimated using the same method.

The behaviour of the confined animals (total number resting, eating pasture, or eating ragwort) was sampled every two minutes for 1-hour on the first and second day of the 10-day confinement period. This method was used to sample the behaviour of the same animals allowed to graze fresh pasture for 1-hour on each of days nine and ten. Both groups were returned to their respective confinement pastures after sampling finished on day nine. The percentage of grazing time spent eating ragwort was analysed with the GLM procedure of SAS (SAS Institute, 1990) after normalisation of the data by arcsine transformation. The proportion of animals in each age/feeding class observed eating ragwort at least once during the observation period was used to determine any age or feeding class effects resulting from confinement.

The positions of ten ragwort plants (5 flowering and 5 rosettes) were marked with numbered stakes in each of the two confinement pastures. Three dimensions for each plant (height, up-slope diameter and across-slope diameter) were recorded and used to approximate a cylindrical volume occupied by the plant. All plants were remeasured on the second, third and tenth day of confinement. The differences in plant cylinder volumes over time were used to approximate the proportion of ragwort material consumed by the sheep in each confinement area. The total volume reduction of each ragwort plant during the 10 days of confined sheep grazing was arcsine transformed and analysed using the GLM procedures of SAS (SAS Institute, 1990). Plant type (rosette or flowering) and feeding class (avid or averse) were the independent variables.

2.3.5. ***Subsequent scan-sampling of lambs*** During the last week of March, 1997, the ragwort eating behaviour of seventeen of the lambs studied in 1996 was observed. Ten of the sheep had previously been classed as avid ragwort eaters, and the remaining seven as ragwort-averse. The behaviour of individual animals was scan sampled (Martin and Bateson, 1986) every two-minutes for 1-hour, during unrestricted grazing as a single flock on ragwort-infested pasture. For each of the 30 scans, the behaviour of each sheep was categorised as either (1) eating ragwort, (2) eating species other than ragwort, or (3) not eating. The flock was observed at 1100-hr for two consecutive days on 25 and 26 March. Each animal had a clearly visible number spray-painted onto both flanks to aid identification. The ragwort feeding by each animal was expressed as a proportion of the total feeding scans (ragwort + other species). These data were averaged over both observation days for each animal and analysed using the GLM procedures of SAS (SAS Institute, 1990).

2.4. Results

2.4.1. ***Proportions of ragwort-averse sheep*** During the initial 10-min of *ad libitum* sampling, 31 ewes and 21 hoggets were not seen eating ragwort. After observing these animals for a further 30-minutes, 15 ewes and 5 hoggets grazed ragwort. This left 11% of the sheep from the ewe flock (n=140) and 16% of the sheep from the hogget flock (n=98) classed as ragwort-averse **(Table 2.1.)**.

Table 2.1. Percentage of sheep from ewe (n=140) and hogget (n=98) flocks not observed to eat ragwort after the 10 and 30-minute sampling periods at Ballantrae, April 1996.

Sampling Period	Ewe (%)	Hogget (%)
First Screening (10 mins)	22	21
Second Screening (30 mins)	11	16

For the lamb flock, 23% were classed as ragwort-averse using the scan-sampling data collected for the experiment described in chapter 3.

2.4.2. ***Indoor ragwort grazing*** The mean dry matter content (DM) of the ragwort leaves presented to sheep indoors was 16.8% for the first sampling period (3-5 April) and 11.9% for the second sampling period (29-30 April).

The mean rate of ragwort consumption indoors by all sheep was greater for the first sampling period (13.5 g/min) than the second (5.8 g/min; $P < 0.01$). There were no interactions between the sampling period and any of the other independent variables (feeding class, age group, or interim grazing regime), indicating that the main effect of less ragwort eating during the second sampling period was consistent for all sheep.

The sheep classed as ragwort-averse consumed less ragwort on average (8.4 g/min) than the avid eaters (10.9 g/min; $P < 0.05$), regardless of age group, during both sampling periods. There was also no interaction between feeding class and interim grazing regime ($P = 0.36$).

A main effect for age group ($P < 0.05$) was also detected. Over both sampling periods hoggets consumed, on average, less ragwort (7.6 g/min) than lambs (11.7 g/min; $P < 0.01$). The ragwort consumption by ewes (9.6 g/min) was intermediate to that of the lambs and hoggets, and did not differ significantly from either of them. (**Table 2.2.**). There were no interactions between age group and the other independent variables.

Table 2.2. Mean (±SE) rate (grams/min) of ragwort consumed indoors by ewes, hoggets, and lambs at Ballantrae, April 1996.

Age Category	Ragwort Consumption (g/min)
Lamb	11.7 ± 1.1 A*
Hogget	7.6 ± 1.1 B
Ewe	9.6 ± 1.1 AB

* Means with different letters differ significantly ($P < 0.01$)

The type of interim grazing regime (confined vs unlimited grazing) did not effect ragwort consumption ($P = 0.31$). As well the absence of a main effect, there were also no interactions between interim grazing regime and any of the three other independent variables.

2.4.3. ***Outdoor confinement comparison*** There was approximately 800 kg of ragwort dry matter per hectare (DM/ha) in each containment area before sheep were released onto them. The pasture dry matter for both areas was initially between 2900 and 3200 kg DM/ha. After the 10 day confinement period the residual pasture mass in the confinement areas was between 1200 and 1400 kg DM/ha.

The proportion of ewes, hoggets and lambs in each feeding class observed grazing ragwort at least once during an observation period remained similar after confined feeding (**Table 2.3.**). A greater proportion of the sheep identified as avid ragwort feeders were observed eating ragwort than those classed as ragwort-averse, and this trend was present both before and after confinement.

Table 2.3. Mean proportion of lambs, hoggets and ewes in each feeding class observed eating ragwort before and after confinement at Ballantrae, April 1996.

	Age Class		
Feeding Class	Lamb	Hogget	Ewe
	Before Confinement (%)		
Averse	36	13	13
Avid	88	50	81
	After Confinement (%)		
Averse	0	25	6
Avid	94	63	94

Collectively, the avid ragwort eaters were observed eating ragwort in 14% of the scan-samples in which grazing (either pasture or ragwort) occurred. In contrast, ragwort eating constituted less than 3% of the total grazing observations for the ragwort-averse sheep. There were no differences in the ragwort proportion of total grazing for each feeding class before or after confinement (**Table 2.4.**).

Table 2.4. Mean percentage of grazing observations where ragwort was consumed for averse and avid eaters before and after confinement at Ballantrae, April 1996.

Feeding Class	Observation Period	Ragwort Grazing (%)
Averse	Before	0.5 A*
	After	3.4 A
Avid	Before	13.9 B
	After	14.1 B

* Means with different letters differ significantly ($P < 0.01$)

The mean cumulative volume (%) of elongated ragwort plants consumed by the two groups of sheep after one, two and 10 days of confinement is illustrated in **Figure 2.1.**. The ragwort-averse sheep did not graze any of the marked elongated ragwort plants during the first two days of confinement. In contrast, the sheep classed as avid ragwort eaters removed 43% of the cylindrical volume of marked elongated plants during the same two day period. After 10 days, the ragwort-averse flock had removed only 42% of the elongated plant volume, significantly less ($P < 0.01$) than the 89% removed by the avid flock.

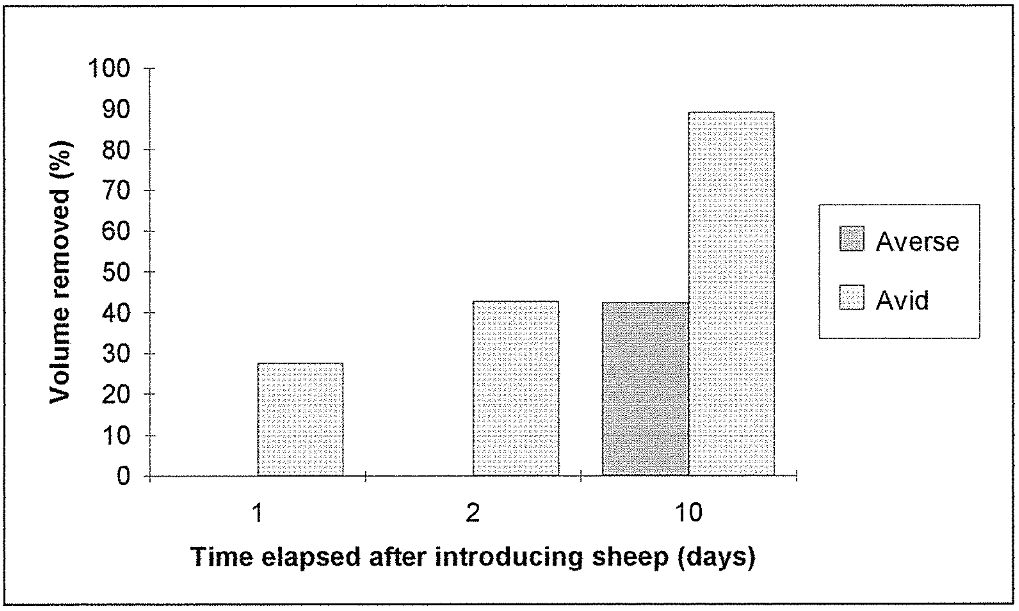

Figure 2.1. Mean cumulative volume (%) of elongated ragwort plants removed by avid and averse sheep after one, two and 10 confinement days at Ballantrae, April 1996.

The pattern of rosette volume reduction in the two confinement areas (**Figure 2.2.**) was similar to that found for the elongated plants during the first two confinement days, with no grazing of marked plants by ragwort-averse sheep during this time. However, by day 10, the ragwort-averse sheep had removed 92% of the rosette volume which was not significantly different ($P = 0.12$) to the 99% removed by the animals classed as avid eaters.

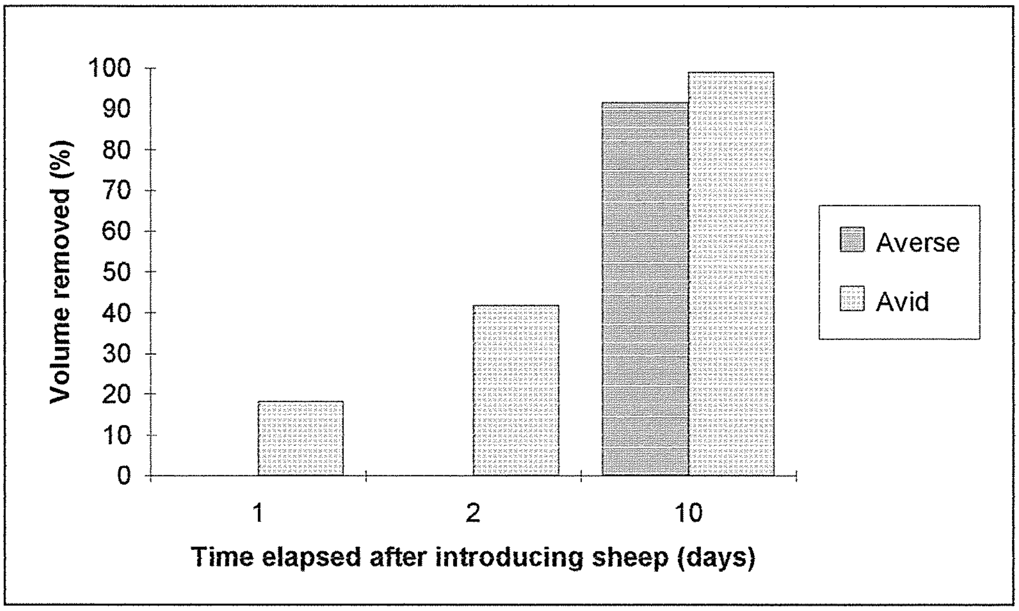

Figure 2.2. Mean cumulative volume (%) of rosette ragwort plants removed by avid and averse sheep after one, two and 10 confinement days at Ballantrae, April 1996.

Within both confinement pastures, the rosette volume removed was greater than the elongated plant volume removed ($P < 0.01$). An interaction between feeding class (avid/averse) and plant type (rosette/elongated) reflected the day 10 difference in elongated plant feeding by avid and averse sheep, but the lack of a similar finding for rosette plants. The day 10 interaction between feeding class and plant type is illustrated in **Table 2.5.**.

Table 2.5. Mean (±SE) percentage of rosette and elongated plant volumes removed by averse and avid ragwort eaters after 10 days of confinement at Ballantrae, April 1996.

	--------------Plant Volume Removed (%)----------	
Feeding Class	Rosettes	Elongated Plants
Avid	99.1 ± 4.8 A*	89.2 ± 4.8 B
Averse	91.5 ± 4.8 A	42.3 ± 4.8 C

* Means within columns and rows with different letters differ significantly ($P < 0.05$)

2.4.4. ***Behaviour of lambs after one year*** There was no difference (P = 0.13) in the ragwort percentage of total grazing scans between the lambs previously identified as ragwort-averse and those classed as avid ragwort feeders. The ragwort percentage of total grazing for the 'avid' lambs (25%) was numerically greater than that for the 'averse' lambs (16%), but the ragwort eating behaviour within each group varied considerably. The relative proportion of feeding behaviour (ragwort or pasture) compared to behaviour other than feeding was similar (P =0.45) for both lamb groups (57% for averse; 69% for avid).

2.5. Discussion

2.5.1. ***Evidence for ragwort aversions.*** The sheep identified as ragwort-averse after initial screening had a lower incidence of ragwort feeding during both the outdoor confinement and indoor feeding experiments than those identified as avid ragwort eaters. This supports the suggestion of Betteridge *et al.* (1994) that some sheep eat less ragwort than others, and that relatively brief *ad libitum* sampling may be sensitive enough to detect these individuals.

Both of the methods used to identify ragwort-averse sheep were effective, although the selection of ewes and hoggets by *ad libitum* behaviour sampling was much faster than the systematic scan-sampling used to provide a detailed behaviour history for the lambs. Because each screening technique used independent criteria to designate sheep as 'ragwort-averse', the proportions determined by them may not be directly comparable. The decreasing proportion of ragwort-averse sheep with increasing age, as indicated by the combination of screening methods, was consistent with ragwort being less toxic to older animals (Cameron, 1935). However, unless these proportions are replicated by screening new sheep flocks with a single standardised procedure, this correlation should be treated with caution.

Betteridge *et al.* (1994) found that 5% of the sheep in a hogget flock appeared not to eat ragwort, compared to 16% for the flock examined in the present study. The screening processes used to derive these proportions were different and may prevent direct comparison. However, the difference may indicate that the proportion of ragwort-averse sheep varies between flocks of similar age and experience. The capacity of individuals of the same species to graze poisonous plants can be extremely variable (Cheeke, 1994).

2.5.2. ***Ragwort feeding behaviour*** The two screening procedures used to identify ragwort-averse sheep defined a ragwort aversion as either "no ragwort eating during 40-mins of observation" or "when ragwort eating does not exceed 2.5% of an activity budget". Both of these definitions apply to free-choice grazing by sheep in ragwort-containing pastures. During the indoor ragwort presentation experiment, where the sheep could either eat ragwort or not feed, the definition of a ragwort aversion changed to "sheep that consumed less ragwort than others when ragwort was the only available food". Thus, the sheep that rarely consumed ragwort during outdoor pasture grazing did consume ragwort when the alternative was not feeding, albeit at a lower rate than the sheep that frequently grazed ragwort in pasture. This implies that an observed reluctance to eat ragwort may be situation-dependent rather than a fixed trait, and that any definition of a ragwort aversion should also define the situation where it occurs.

The situational factors that may influence ragwort eating include not only the external environment, but also the internal environment (state) of the sheep. For example, hungry animals tend to eat at a faster rate than less hungry animals (Newman *et al.*, 1994). In the indoor ragwort presentation experiment, all sheep consumed less ragwort during the second testing period than the first, with the sheep classed as avid eaters still consuming more than those classed as ragwort-averse. One possible explanation for the drop in ragwort consumption is that the hunger levels of the sheep may have been greater during the first period of indoor testing than the second. During the training period before the indoor presentation of ragwort, all the sheep were kept in holding pastures adjacent to the wool shed. The sheep grazed these pastures for the five days of indoor training and a for a further three during the initial ragwort acceptance tests. Although no pasture measurements were taken, the grass became visibly depleted during this eight day period. In contrast, the holding pastures used during the second period indoors had better grass cover and the animals were retained on them for only two days. Sheep may become less reluctant to eat a non-preferred food the longer they are fasted (Dumont and Petit, 1995). If the sheep were hungrier during the first period of indoor ragwort presentations, it did not increase the acceptance of ragwort by the averse sheep relative to that of the avid sheep, compared to the second testing period.

A problem with making cross-sectional behaviour comparisons between animals of differing age is that observed differences may result from the shared experiences of a specific cohort group that may not represent the behaviour of most other individuals of the same age (Martin and Bateson, 1986). During the indoor experiments, the lambs consistently consumed more ragwort than the hoggets, regardless of feeding class. This difference could be attributed to a greater acceptance of ragwort by lambs. However, lambs usually consume less ragwort than older sheep (Cheeke, 1984). Instead, the difference may reflect greater habituation by the lambs to feeding in the presence of humans as a result of their previous experimental history (Martin and Bateson, 1986). Compared to the hoggets, the lambs were much easier to handle, and less wary of experimenter presence. Most of the lambs began eating immediately after the feed tray was placed in the pen, whereas the hoggets usually waited until the experimenter had disappeared from view. The hoggets had no previous experimental history.

From a ragwort control perspective, the differences in behaviour of the ragwort-averse sheep and the avid eater flock, while confined on ragwort containing pasture, were of practical importance. Specifically, the ragwort-averse sheep did not graze any of the marked ragwort plants during the first two days of confinement, whereas the avid ragwort eaters affected a 45% volume reduction during the same period. This suggests that screening sheep for ragwort eating may quickly separate individuals that almost immediately graze ragwort from those that will not graze it before first depleting other pasture species. Being able to reliably identify these individuals may allow smaller flocks of avid eaters to be used for ragwort control in place of larger flocks containing redundant animals. However there are potential problems with the 40-min *ad libitum* screening procedure and replication is required to assess its reliability. One possible source of screening errors is that sheep often sample non-preferred food at very low rates (Thorhallsdottir *et al.*, 1987). If the screening procedure is used only to identify avid eaters, then this will not be a problem, however, if a farmer is wanting to sell off the averse eaters in a flock, then a rare ragwort eating event coinciding with screening could result in the retention of a relatively ragwort-averse individual.

After 10 days, all of the rosettes in both confinement pastures were grazed to ground level, and the elongated plants were reduced to short (~15cm) stalks by the avid eaters. The ragwort-averse sheep did not graze the woody elongated plants as heavily as the avid eaters after 10 confinement days, although they did remove a similar amount of rosette material, which may support Cameron's (1935) contention that the rosette stage is more palatable. However, the avid sheep removed similar volumes of rosette and elongated plants after 2 days of grazing, suggesting that the relationship between plant stage and palatability may be more complicated. *Ad libitum* data collected between scan samples during the first and second days of confinement suggest that some of the avid sheep may preferentially graze flower heads while others strip the leaves from both rosette and elongated plants.

2.5.3. ***Robustness of ragwort feeding behaviour.*** Poole and Cairns (1940) suggested that sheep initially reluctant to eat ragwort often develop a preference for the plant after being compelled to eat it. This observation applied to sheep that had never grazed ragwort before, whereas the sheep used for the present study had been reared on ragwort pasture since birth. Mature sheep are often reluctant to accept novel foods, although once they lose this neophobia they often develop preferences for them (Chapple and Lynch, 1986). With sheep reared on pasture containing ragwort, strong ragwort aversions or preferences are likely to have developed from an early age that may be resistant to modification.

Ragwort-averse sheep will eat ragwort indoors if no other food is available, although they eat collectively less than sheep classed as avid ragwort eaters. After consuming ragwort during the indoor acceptance tests, ragwort-averse sheep failed to graze ragwort in an outdoor confinement paddock until other pasture species were depleted. Thus the initial period indoors did not increase the initial ragwort feeding of averse sheep. There was also no evidence of increased ragwort feeding when ragwort-averse sheep grazed fresh pasture after 10 days of confinement during which they were compelled to eat ragwort. This may reflect a tendency for sheep to select plant species different to those most recently experienced when free-choice grazing is reinstated (Parsons *et al.*, 1994). If the averse sheep had grazed mostly ragwort immediately before day 10, then this tendency may have masked any change in ragwort feeding behaviour. This may also apply to the avid eaters because it is possible that they depleted most of the ragwort well before day 10 and had been feeding predominantly on other pasture species immediately before observation. Thus, the avid ragwort eating displayed by these sheep, when introduced onto fresh pasture, may be consistent with a tendency to consume a food type not recently eaten. However, this type of preference often disappears within a day (Parsons *et al.*, 1994), and the second set of indoor trials showed that ragwort-averse sheep, despite being compelled to eat ragwort first indoors and then during outdoor confinement, still consumed proportionately less ragwort than the sheep classed as avid eaters. The ragwort eating behaviour of ragwort-averse sheep and avid ragwort eaters was not easily modified and therefore remained consistent during all of the 1996 studies.

The observations made in 1997 of some of the experimental lambs (now hoggets) from the previous year suggested that the animals originally classed as ragwort-averse now consumed ragwort as frequently as the lambs classed as avid eaters. This finding may indicate that ragwort feeding preferences of sheep are not constant over time. However, lambs may be a special case. Ragwort is more toxic to lambs than it is to mature sheep and as lambs develop they are able to eat progressively more of it (Cheeke, 1984). Because development varies between individual sheep (Cheeke, 1994), some of the lambs that appeared to be reluctant ragwort eaters in 1996 may have had a less developed capacity to graze it safely than those originally classed as avid eaters. The 1997 observations may illustrate an acquired tolerance to ragwort rather than a simple change in preference by the originally reluctant lambs.

Longitudinal studies of mature sheep are needed to determine the long-term robustness of observed ragwort aversions. This study suggests that ragwort feeding by sheep appears relatively resistant to modification in the short-term. A farmer considering the purchase of sheep for ragwort control needs confirmation that the sheep readily graze ragwort before buying them, because the preference of the sheep for ragwort, be it avid or averse, is likely to be resistant to change.

Chapter Three

Can the Rearing Conditions for Lambs Increase Ragwort Grazing?

3.1. Introduction

A sensitive period in development is an age range when specific experiences are most likely to affect an individual's development (Martin and Bateson, 1986). The grazing experiences of lambs before weaning influence their food preferences as adult sheep (Ramos and Tennessen, 1992). Lambs that grazed leafy spurge (*Euphorbia esula* L.) before weaning consumed more of it after weaning than did naive lambs (Walker *et al.*, 1992). Dietary preferences of lambs may also be modified by maternal influences (Nolte *et al.*, 1990). Key and MacIver (1980) found that after cross-fostering lambs between two sheep breeds that the lambs later preferred the food eaten by their foster mothers. Lambs that feed with their mothers before weaning often display food preferences similar to the mother's after weaning (Thorhallsdottir *et al.*, 1990a). Thus, lambs that graze ragwort with their mothers before weaning may eat more ragwort after they are weaned than lambs with no previous ragwort experience. Clarifying this possibility would be useful from the perspective of controlling ragwort.

Following weaning, the food preferences of lambs can be influenced by grazing with older sheep (Chapple and Lynch, 1986) or other lambs (Scott *et al.*, 1996). Weaned lambs can learn how to eat novel foods from any sheep already eating it (Chapple and Lynch, 1986). Poole and Cairns (1940) found that sheep from non-ragwort country initially avoided eating ragwort. Lambs with a ragwort-free grazing history may also be reluctant to eat ragwort. However, obtaining some of these 'reluctant' lambs for immediate ragwort control may be an option if sheep that already graze ragwort are present to 'teach' the new arrivals.

3.2. Objectives

To determine:

(1) The effect of pre-weaning ragwort exposure on the subsequent grazing of ragwort by lambs.

(2) The effect of grazing with ragwort-eating ewes during weaning on the subsequent grazing of ragwort by lambs, with or without, previous ragwort grazing experiences.

3.3. Methods and Materials

3.3.1. *Study area* The experiment ran over three months on hill country farmland at the AgResearch Ballantrae Research Station (36°S) near Palmerston North, New Zealand.

3.3.2. *Formation of treatment groups* Sixty pregnant Romney ewes with a history of grazing on ragwort infested pastures were provided by AgResearch. Thirty ewes were randomly selected and transported to Flock House, a ragwort-free farm, in mid-August (early spring) 1995. The remaining 30 ewes continued to graze on ragwort-containing pasture at Ballantrae. Lambing began in early September, and lambs were reared with their mothers on their respective pasture types.

On 14 November 1995 the ewes and lambs on ragwort-free pasture were returned to Ballantrae and retained on pasture cleared of ragwort. Twenty-four hours later the lambs from both background pasture types were weaned by swapping the ewes between the two groups. Each group of lambs was split into two using a weight-restricted randomisation. Only the 15 heaviest lambs from each of the four resulting groups were selected for experimental observation. During the experiment one group of lambs from each of the two pasture backgrounds was confined with six ewes from the opposite pasture background. Thus, 15 lambs from ragwort-containing pasture were confined with ewes that had not grazed ragwort infested pasture from lambing, and 15 lambs from ragwort-free pasture with ewes that had recently grazed ragwort infested pasture. The ewes in both lamb + ewe groups were selected because they displayed the greatest propensity for eating ragwort when cut plants were offered to each ewe flock in sheep-yards. The two remaining lamb groups grazed without ewes.

All lambs were individually identified with numbered ear-tags. All the lambs from ragwort-containing pasture had blue ear-tags, and those from ragwort-free pasture had purple ones, to enable fast identification of background pasture type. In addition to ear-tags, all lambs were spray-painted with a number (1-15) on each shoulder, side, and rump (**Plate 4**), with lambs confined with ewes being sprayed with red paint and those that grazed alone with blue. The 12 ewes were similarly marked.

The lambs born on ragwort-free pasture were retained on similar pasture (no ragwort) for two weeks at Ballantrae, before observations on ragwort infested pasture began on 27 November 1995.

Plate 4. Lambs with freshly painted numbers, grazing amongst elongated ragwort plants.

3.3.3. ***Experiment Design*** Four 10-m wide pasture lanes were created with electric sheep netting in a paddock infested with ragwort. Care was taken to ensure that ragwort content and size distribution both between and within lanes was similar. Each lane was divided into daily grazing areas sufficient for 24-hour feeding to provide moderate animal growth, but less than *ad libitum* feeding. Lambs with ewes present were given larger areas (~130-m^2) than lambs grazed alone (~100-m^2). Sheep were introduced into a new pasture area immediately prior to observational recording.

Plant measurements and animal observations were made during three separate observation periods; Week 1 (immediately following weaning), Week 3, and Week 12. Five days of observation were made during Week 1, and four days of consecutive observation were made during Weeks 3 and 12. The ewes were removed from their respective lamb groups immediately prior to the first observation day of Week 12. All four groups were grazed separately from Week 1 through to Week 12 both during and between observation periods. Each of the four sheep groups grazed a fresh lane of pasture during each observation week. selected randomly,

The lanes used during Weeks 3 and 12 were set up in a separate area of the farm to that used in Week 1. This unplanned change in locality occurred because a flock of mature ewes grazed the Week 1 paddock between Weeks 1 and 3, and effectively removed all the ragwort.

3.3.4. ***Animal Measurements*** All of the 4 groups were observed for 1-hour on each observation day. Because of a limited number of observers (n=5), only two groups could be sampled at the same time. For each observation day the order for sampling the groups was randomised to allow for any time-of-day effects.

At 0900-hr (or 1030-hr) two observers collectively scan-sampled (Altmann, 1974) 1 group of lambs at two-minute intervals. One observer made the observations while the other recorded them. This provided 30 scan-samples of the group for each observation day. During a scan each individual was categorised as (1) eating ragwort, (2) eating a plant other than ragwort, or (3) not eating. A third observer recorded the same activities for the ewes (if present).

One-minute focal samples (Altmann, 1974) of specific lambs (and ewes) in each group were made alternately with the scan-samples (**Plate 5**). The same behaviour categories as those used for scan-sampling were used for focal-sampling. Each observer used a dictaphone to record when the behaviour of the lamb changed from one of the three categories to another. The time spent by the lamb engaging in each behaviour was determined after real-time transcription from cassette to computer spreadsheet. Each observer focal sampled the behaviour of three lambs during each 1-hr sampling period. For every set of three focal samples, the order for observing each of the focal animals was randomly determined before sampling began. This provided 10 one-minute records of behaviour for six focal lambs (and three focal ewes when present) in each lamb group per observation day. The proportion of total grazing time spent eating ragwort was the dependent variable for analysis.

Plate 5. Focal-sampling of lambs and ewes confined in a daily grazing area.

For both the scan and focal samples, the proportion of total grazing scans or time (ragwort + pasture) where ragwort was the plant consumed was used as the dependent variable for analysis. The main effects of sampling period (Week), presence of a ewe, and background pasture type on the dependent variable were assessed using the GLM procedures of SAS (SAS Institute, 1990). Any interactions between the independent variables were also examined. For the purpose of analysis, the experimental units were the individual lambs. The repeated observations for each lamb within each week were averaged to give a single value per lamb for Weeks 1, 3 and 12. An arcsine transformation was performed on the data before analysis to stabilise the variance of the group means. The same procedures were used for a separate analysis of the ewe data.

3.3.5. ***Plant Measurements*** Within each daily grazing area, 20 ragwort plants were identified with a numbered peg, and the height and two width dimensions at ground level (taken at right-angles to each other) were recorded. The growth stage of each plant was also noted, and categorised as either rosette or elongated. These initial plant measurements were completed before the sheep were let into the grazing area for 24-hours. Plant volumes were estimated on the assumption that the plants were cylindrical in shape and that reduction in volume equated to ragwort consumption. These measurements were repeated once animals were removed from the plot after 24 hours of confinement. The mean volume of ragwort material removed per day by each group during each week was analysed using the GLM procedures of SAS (SAS Institute, 1990). Sampling period (Week), previous grazing with ewes and background pasture type were the independent variables. The effect of plant growth stage on the same dependent variable was analysed in a separate, but similar analysis.

Mean pasture height was determined from 50 'first hit on green stem' sward stick measurements made daily in each lane. Pasture mass was estimated from Ballantrae calibrations of height against pasture dry matter (DM) following the method used by Webby and Pengelly (1986).

3.4. Results

3.4.1. ***Pasture measurements and lamb weights*** The mean ragwort plant heights measured during Weeks 1, 3, and 12, were 25, 29, and 48-cm respectively; and the mean volumes were 0.26, 0.22, and 0.29-m^3. The ragwort heights and volumes were similar between lanes within each week (week × group interaction; $P = 0.35$). Mean grass height, before grazing, was 16, 13, and 11-cm (3100-2100 kg of Dry-Matter per ha) in each period respectively, and the 24-hour post-grazing height reduction was always between 46 and 48%. Each lane contained an average of six non-seedling ragwort plants per square metre.

The average weaning weight of the lambs was 20-kg and this increased to 29.7-kg at the conclusion of Week 12.

3.4.2. ***Scan sampling of lambs*** For all lamb groups the mean percentage of ragwort-feeding-scans was similar during Week 1 (**Table 3.1.**). The mean for the lambs from the ragwort-free background that grazed without ewes was numerically, but not significantly ($P = 0.10$), lower than the other groups. During Week 3 the ragwort grazing by the lambs confined with ewes was greater than those that grazed alone ($P < 0.05$), regardless of the background pasture (**Table 3.1.**). Both lamb groups with ewes present increased their ragwort grazing from Week 1 to Week 3 ($P < 0.05$), whereas the ragwort grazing of lambs without ewes remained static ($P = 0.92$). The mean ragwort component of grazing was always less than 3% during Weeks 1 and 3.

Table 3.1. Mean percentage (±SE) of feeding scans spent eating ragwort by lambs from ragwort-free (naive) or ragwort-present (exposed) pasture, grazing with or without ewes during Weeks 1, 3 and 12, at Ballantrae 1995-96.

	-----------Exposed (%)--------		-------------Naive (%)*-------	
Week	Ewes present	Ewes absent	Ewes Present	Ewes absent
1	0.84 ± 0.2 A	0.76 ± 0.2 A	0.53 ± 0.2 A	0.05 ± 0.2 A
3	2.51 ± 0.3 B	0.54 ± 0.3 A	1.27 ± 0.3 B	0.30 ± 0.3 A
12	7.07 ± 2.0 C	6.60 ± 2.0 C	8.28 ± 2.0 C	7.62 ± 2.0 C

* Means within rows and columns with similar letters are not significantly different ($P < 0.05$)

By Week 12 all of the lamb groups spent significantly more time grazing ragwort compared to the first two sampling periods. There were no differences in ragwort grazing between groups during Week 12 (**Table 3.1**).

3.4.3. ***Focal sampling of lambs.*** For Weeks 1 and 3 the focal animals from each group spent similar amounts of time grazing ragwort, except for those from the ragwort-free background that grazed alone. This group spent less time grazing ragwort (P < 0.05) than the others during both weeks (**Table 3.2.**). The lambs from the ragwort-free background that grazed with ewes spent more time grazing ragwort during Weeks 1 and 3 than the lambs from the same background that grazed without ewes. Compared to the scan-sample data (**Table 3.1.**) the focal animals from the groups that grazed with ewes did not spend more time grazing ragwort during Week 3 than those that grazed alone (P = 0.16).

Main effect ?

Table 3.2. Mean percentage (±SE) of feeding time spent eating ragwort by lambs from ragwort-free (naive) or ragwort-present (exposed) pasture, grazing with or without ewes during Weeks 1, 3 and 12, at Ballantrae 1995-96.

	-----------Exposed (%)--------		-------------Naive (%)*-------	
Week	Ewes present	Ewes absent	Ewes Present	Ewes absent
1	0.17 ± 0.4 A	large (·4)? 1.52 ±A	0.66 ± 0.4 A	0.00 ± 0.4 B
3	1.38 ± 0.4 A	1.25 ± 0.4 A	0.79 ± 0.4 A	0.05 ± 0.4 B
12	7.89 ± 2.0 C	3.91 ± 2.0 C	9.13 ± 2.0 C	7.00 ± 2.0 C

* Means within rows and columns with similar letters are not significantly different (P < 0.05)

The proportion of time spent grazing ragwort in Week 12 was greater than the previous weeks (P < 0.01) for all groups (**Table 3.2**). There were no differences between groups during Week 12, although the mean for lambs from ragwort-containing pasture that grazed without ewes is numerically lower than the other groups. The Week 12 ragwort grazing percentages derived from both types of behaviour sampling are numerically similar, with means of 6.9% for focal-sampling and 7.4% for scan-sampling (averaged data for all four lamb groups during Week 12).

3.4.4. ***Plant volume reduction*** The mean percentage of ragwort removed from the grazing areas after 24-hours increased from Week 1 to 3, and from Week 3 to 12 ($P < 0.05$), for the two lamb groups that grazed without ewes (**Table 3.3.**). The lambs from the ragwort-present background consumed more ragwort than those from the ragwort-absent background ($P < 0.05$) during both Weeks 1 and 3. The focal animal sampling indicated a similar difference (**Table 3.2**). There is no ragwort volume reduction data for the lamb + ewe groups during Weeks 1 and 3 because the individual contributions of the lambs and ewes cannot be separated.

Table 3.3. Mean percentage (±SE) of ragwort volume reduced after 24-hour grazing periods by lambs from ragwort-free (naive) or ragwort-present (exposed) pasture, grazing with or without ewes during Weeks 1, 3 and 12, at Ballantrae 1995-96.

	-----------Exposed (%)--------		-------------Naive (%)---------	
Week	Ewes present	Ewes absent	Ewes Present	Ewes absent
1	-	27 ± 6 A*	-	4 ± 6 B
3	-	39 ± 6 B	-	21 ± 6 A
12	51 ± 4 C	61 ± 4 C	65 ± 4 C	60 ± 4 C

* Means within rows and columns with similar letters are not significantly different ($P < 0.05$)

Week 12 ragwort consumption was similar for all groups, which agrees with the data compiled from both of the animal sampling methods.

3.4.5. ***Ewe behaviour*** Both the focal- (**Table 3.4.**) and scan-sampling (**Table 3.5.**) data show that the ewes that grazed with lambs from the ragwort-present background spent more time eating ragwort than those that grazed with lambs from the ragwort-free background, during Weeks 1 and 3 ($P < 0.05$). There was also an interaction between week and ewe group ($P < 0.01$), with the ewes that grazed with lambs from ragwort-containing pasture spending more time grazing ragwort during Week 1 than Week 3, compared with no difference for the other ewe group (**Tables 3.4.** and **3.5.**).

Table 3.4. Mean percentage (±SE) of feeding scans spent eating ragwort by ewes that grazed with lambs from ragwort-free (naive) or ragwort-present (exposed) pasture during Weeks 1 and 3 at Ballantrae, 1995-96.

	----------Lamb group that ewes grazed with--------	
Week	Exposed (%)	Naive (%)
1	20.4 ± 1.6 A*	3.5 ± 1.6 C
3	11.8 ± 1.6 B	6.2 ± 1.6 C

* Means within rows and columns with similar letters are not significantly different ($P < 0.05$)

The percentage values presented in **Tables 3.4** and **3.5.** are similar, although those derived from focal-sampling are based on half the number of subjects than the scan-sampling means.

Table 3.5. Mean percentage (±SE) of feeding time spent eating ragwort by ewes that grazed with lambs from ragwort-free (naive) or ragwort-present (exposed) pasture during Weeks 1 and 3 at Ballantrae 1995-96.

	----------Lamb group that ewes grazed with--------	
Week	Exposed (%)	Naive (%)
1	28.8 ± 2.5 A*	2.8 ± 2.5 C
3	10.2 ± 2.5 B	3.4 ± 2.5 C

* Means within rows and columns with similar letters are not significantly different ($P < 0.05$)

3.4.6. *Ragwort growth stage preferences of lambs* An analysis of the mean volume of rosettes and elongated ragwort plants consumed by lambs during Week 12 detected an interaction between plant type and the background pasture of the lamb. The lambs from ragwort-free pasture consumed more rosette material (85%) than those from ragwort-present pasture (59%; $P < 0.01$). Both lamb groups consumed 54% ($P = 0.42$) of marked elongated plants during Week 12 (**Figure 3.1.**).

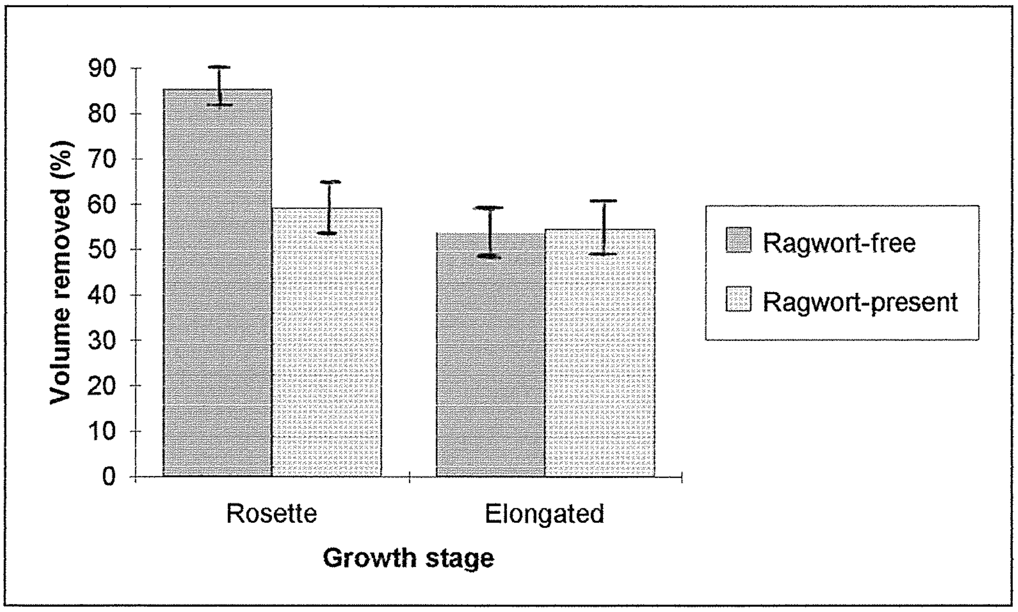

Figure 3.1. Mean volumes (%) of rosette and elongated ragwort plants removed during Week 12 by lambs from ragwort-free and ragwort-present pasture backgrounds at Ballantrae 1995-96.

3.4.7. ***Activity Budgets*** The combined focal ewe data and that for the focal lambs during Week 12 were averaged to produce a pictorial illustration (**Figure 3.2.**) of the proportion of time spent grazing ragwort, grazing pasture, and activities other than grazing, for each age group. The patterns appear similar, except the ewes may spend relatively more time than lambs on activities other than grazing, although these data were not analysed statistically. During the first hour of access to fresh pasture lambs spent 82% of the time grazing (ragwort and pasture), compared with 72% for the ewes.

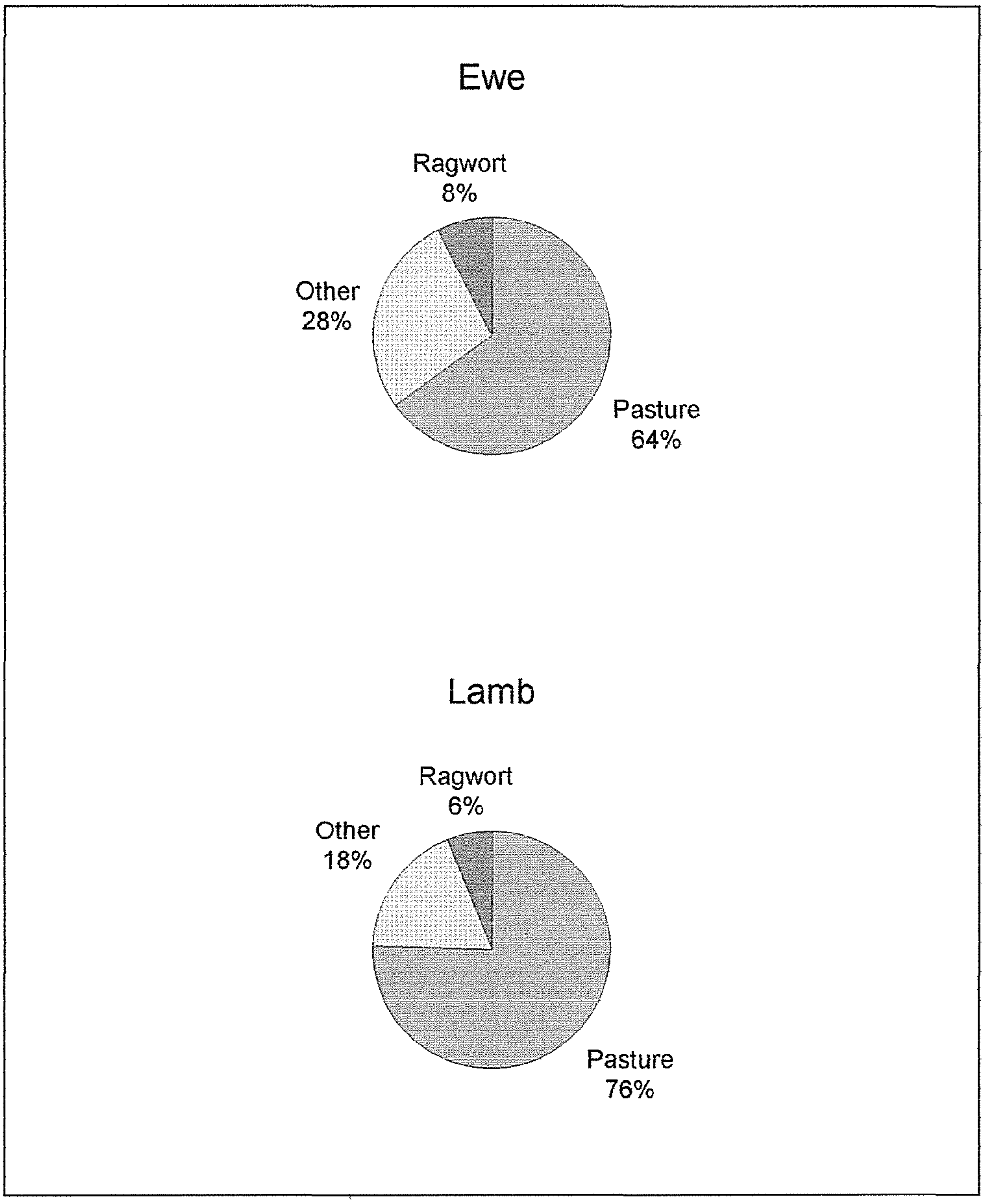

Figure 3.2. Relative proportions of grazing on ragwort, grazing on pasture, and activities other than grazing for the combined focal ewe data and the focal lamb data from Week 12 at Ballantrae 1995-96.

3.5. Discussion

Focal lambs
Exp > Naive
but not Scan.

3.5.1 ***Sampling issues*** Lambs reared to weaning on ragwort-containing pasture removed more ragwort per day during the first and third weeks after weaning than lambs reared without exposure to ragwort. This difference was indicated by the focal animal data, but not by the data collected with scan-sampling. This disagreement between the animal sampling methods probably relates to the low frequency of ragwort consumption by a limited number of lambs during the first hour of grazing fresh pasture in both Weeks 1 and 3.

Scan-sampling is usually unreliable for recording the frequency of rare behaviour events (Martin and Bateson, 1986). The method depends on recording the behaviour being performed by an individual at the exact instant the individual is observed. For the present study, ragwort-eating was the behaviour of interest and because of its unanticipated initial rarity, observers may have recorded occurrences that happened slightly before or after each sampling point. This would have the effect of overestimating ragwort-eating behaviour. Also, observers with knowledge of possible treatment effects may unwittingly be more lenient with the instantaneous samples of the groups expected to show the greatest incidence of the target behaviour, and, especially with rare behaviour, this can produce a treatment effect where none exists (Kalat, 1990).

In comparison, focal animal sampling can accurately sample rare events, and is reliable as long as the observed animals behave similarly to others in the same group (Martin and Bateson, 1986). Unfortunately, ragwort eating did vary between lambs. However, the practice of focal-sampling six individuals from each group was expected to approximate group behaviour. The similarity of the Week 12 scan- and focal-sampling percentages suggests that this assumption was valid, because scan-sampling probably became a more reliable benchmark for comparison when ragwort eating became more frequent in Week 12.

Focal sampling is, however, susceptible to the effects of untrained observers (Martin and Bateson, 1986). During the first week of sampling it is possible that some recorded instances of ragwort feeding were actually lambs removing grass from the base of ragwort plants. Ragwort can facilitate the growth of some pasture species in its immediate vicinity by providing an improved microclimate and protection from grazing by cattle (Wardle *et al.*, 1995). Lambs were able to selectively graze this lush pasture, especially within large multi-stemmed plants, without ingesting ragwort. However, the lambs did tend to shake the plants as they selected the grass stems, and this shaking was probably intermittently recorded as ragwort feeding during the first week of observation, giving an overestimate of ragwort feeding.

A further problem with observing the ragwort feeding behaviour of lambs is that it was easier to observe the grazing of elongated plants than of low growing rosettes. As observers became more experienced, increased rosette grazing was probably recorded. This implies that observations made during Week 1, may underestimate ragwort feeding, because of missed instances of rosette grazing. Seedling grazing was completely ignored because, apart from being virtually impossible to detect by eye, seedlings are small enough to escape grazing by sheep until they reach small rosette size (Watt, 1993).

A possible source of error with the plant measurements is the assumption that grazing damage equated to consumption. Although grazing by sheep was clearly distinguishable from other sources of plant damage such as treading or cinnabar moth defoliation, some lambs severed ragwort leaves and then dropped them to gain clear access to the lush grass growing at the base of ragwort plants. Large rosette plants appeared most affected by this grazing pattern because lambs could push into the middle of large elongated multi-stemmed plants without grazing them. This may have resulted in the overestimation of rosette consumption.

In summary, focal- and scan-sampling were possibly unreliable during Week 1 because of inexperienced observers. The rarity of ragwort feeding may also extend the unreliability of scan-sampling to Week 3, although the focal sampling does not suffer from the same bias. This suggests that the increase in ragwort feeding by lambs with ewes from Week 1 to Week 3 that is present only in the scan-sampling data could be unreliable. In contrast, the lower incidence of ragwort grazing by the lambs that grazed without ewes from ragwort-free pastures, compared with their counterparts from the ragwort-present pastures is a pattern shown by both the plant volume data, and the focal animal sampling, and probably represents a reliable effect of pre-weaning ragwort exposure on post-weaning ragwort grazing.

3.5.2. ***Ragwort exposure before weaning*** Exposure to ragwort with their dams before weaning increased the grazing of ragwort immediately after weaning by lambs that grazed without ewes. This measured difference in ragwort utilisation by the lambs from each pasture background supports an assumption of the present research; that the lambs reared on ragwort-containing-pasture actually did sample ragwort prior to weaning. This is important because previous research suggests that simply exposing lambs to a new food has little effect on later food preferences, unless sampling of the food occurs (Chapple and Lynch, 1986). Reduction in ragwort volume was observed in the ragwort-containing-paddocks occupied by the ewes and their lambs before weaning (J.Napier, pers. comm.). This would have produced an environment where the lambs had many opportunities to interact with ewes eating ragwort. This lends further support to the assumption that the unweaned lambs experienced ragwort during their exposure to it. Participating with a grazing mother has an even greater influence on the later food preferences of unweaned lambs than learning through trial and error alone (Thorhallsdottir et al. 1990a), and may have contributed to the greater consumption of ragwort by the ragwort-exposed lambs during Weeks 1 and 3. However, the relative effects of individual ragwort-eating experiences and grazing ragwort with a mother before weaning are inseparable in the present study.

3.5.3. ***Diurnal preference patterns*** The animal measurements did not detect the increase in ragwort grazing from Weeks 1 to 3 shown by the plant volume reduction data for both groups of lambs that grazed alone. This may, as discussed in 3.5.1., be due to an overestimation of ragwort grazing by the focal- and scan-sampling methods used in Week 1. However, a second possibility is that the 1-hr animal observations and the 24-hr plant measurements are not equivalent measures of ragwort grazing by the lambs. Ragwort plants were rarely grazed by both lamb groups through each one hour observation period during Weeks 1 and 3. Instead, as soon as the lambs were released onto a new grazing area they immediately began to graze other pasture species such as Lotus and Yorkshire Fog. During Weeks 1 and 3 the lambs from the ragwort-present pasture usually grazed ragwort sometime after the observation period had finished, as did the lambs from ragwort-free pasture during Week 3. The lambs from ragwort-free pasture grazed very little ragwort at any time during Week 1. This finding, that short-term observations of grazing behaviour, made at a single time of day, may not represent longer-term grazing patterns, has been found by Parsons *et al.* (1994) with Scottish halfbred ewes that exhibited changing preferences for clover and ryegrass.

There are at least two alternative explanations for the possible increase in ragwort eating initially displayed by the ragwort-exposed sheep after the first hour on new pasture. The first is that ragwort may not have been a preferred food for the lambs and therefore remained relatively untouched until more preferred species were depleted, and/or rendered inedible through trampling. Walker *et al.* (1992) found that lambs avoided grazing leafy spurge when other pasture species were readily accessible, but switched to grazing leafy spurge when its biomass was high relative to other pasture species. A second possibility is that ragwort was not preferred by ragwort-exposed lambs in the morning, but was taken at some time later in the day. This type of regular diurnal preference pattern, for reasons other than the depletion of a previously preferred species, could indicate a determined strategy of ingestion (Sibley, 1981). Both possibilities are equally likely, and distinguishing between them would involve observing lambs grazing on large areas of pasture, to ensure the maintenance of free-choice grazing throughout each 24-hour period of confinement (Parsons *et al.*, 1994). Further, both possibilities require the ragwort-exposed lambs to have sampled ragwort before weaning, and to have developed a learned response that persisted after weaning in a familiar grazing environment (Scott *et al.*, 1996). In contrast, lambs reared on ragwort-free-pasture probably grazed only familiar species when first exposed to ragwort (a novel plant) in an environment that was initially unfamiliar to them (Scott *et al.*, 1996); and ragwort remained relatively untouched as a consequence.

3.5.4. ***Social facilitation by ewes*** Social facilitation occurs when a learned behaviour is performed at a greater rate when animals co-act with other individuals, than when the behaviour occurs in the absence of others (Thorhallsdottir *et al.*, 1990b). During Weeks 1 and 3, the focal animal sampling indicated that the presence of ewes facilitated the sampling of ragwort by lambs from ragwort-free pasture. The time spent eating ragwort by these lambs was similar for both groups reared on ragwort-present pasture and greater than for the lambs from the same background that grazed alone. The relative contributions of social facilitation and persistent learned preferences to this increased eating of ragwort are inseparable, because the lambs from ragwort-free pasture always grazed with the ewes during Weeks 1 and 3. It is therefore unknown whether the increased level of ragwort sampling by the lambs would have persisted in the absence of the ewes. There was no difference in the Week 12 percentage of ragwort volume removed over 24-hours by any of the lamb groups, suggesting that ewes may have initially facilitated the eating of ragwort by lambs from ragwort-free pasture without increasing its long-term inclusion in their diet.

The focal animal sampling suggested that the presence of ewes did not facilitate ragwort-eating by the lambs from the ragwort-present pasture background. This was not unexpected because these lambs had previously grazed ragwort-containing pastures with their mothers during the sensitive developmental period before weaning, suggesting that the lambs would already have developed a pattern of ragwort ingestion (Thorhallsdottir *et al.*, 1990a).

3.5.5. ***Persistence of exposure and ewe effects*** Ragwort-eating, in comparison to other feeding, increased substantially between Weeks 3 and 12 for all four lamb groups. This pattern of initial low intake of a food type by lambs, followed by a large increase in consumption is a regularly reported finding; eg Chapple and Lynch (1986) with wheat; and Ralphs *et al.* (1990) and Pfister & Price (1996) with locoweed, a plant which, like ragwort, also contains toxic alkaloids. The gradual process of habituation to a novel food is one possible interpretation of the increase (Ralphs *et al.*, 1990). This, however, fails to explain why lambs exposed to ragwort from birth underwent an increase similar in magnitude to the lambs that remained unexposed until after weaning. Because of the data gap between weeks 3 and 12 we do not know: when the marked increase in ragwort-eating during this period occurred; whether the transition was sudden or gradual; and whether the pattern was the same for each group.

Thus it is unclear if the lambs in all four groups independently reached an experience threshold after which ragwort grazing increased markedly and further grazing experience became less important. For example, once sheep eat more than 10g of wheat during daily, 15-min feeding sessions, wheat-eating increases very rapidly (Chapple and Lynch, 1986). The difference between the lambs that grazed without ewes from ragwort-free and ragwort-present pastures in the volume of ragwort consumed did not persist into Week 12, suggesting that 12 weeks of exposure to ragwort may have allowed the lambs from the ragwort-free background to develop similar ragwort grazing skills to those reared with their mothers on ragwort-present pastures. However, a second variable that may determine the amount of ragwort included in the diet of lambs is age. Unfortunately, age is confounded with experience so that the relative effects of the two variables can only be speculated.

Young animals are generally more susceptible to ragwort pyrrolizidine alkaloid (PA) toxicosis than older ones, because of increased cellular activity and higher levels of PA bioactivating enzymes in the liver (Johnson *et al.*, 1985). Furthermore, lambs are more susceptible than older sheep to the toxic effects of excess ragwort ingestion (Cameron, 1935; Olson and Lacey, 1994). Possibly the lambs used in the present study developed an increased tolerance for PAs between Weeks 3 and 12 that enabled them to eat more ragwort. This could have occurred through a combination of factors, including a decline in PA bioactivating enzymes, an increase in PA detoxifying enzymes in the liver (Cheeke, 1994) and/or development of rumen microflora (Wachenheim *et al.*, 1992).

Physiological changes that allow the ingestion of toxic foods may not only occur as a result of developmental processes; but may also occur as an adaptive response to a major change in forage type (Olson and Lacey, 1994). Such adaptations could also involve changes in rumen microflora and/or the relative concentrations of enzymes in the liver (Olson and Lacey, 1994). This may help to explain the observation by Poole and Cairns (1940) that adult sheep with no ragwort experience tend to eat very little of the plant initially (unless forced to eat it through a lack of alternative forage) until, after continued sampling, a taste for the plant rapidly develops; and it eventually becomes a large component of the diet.

Clearly, further research should aim to separate the relative effects of age, physiology, and learning, on the level of ragwort-eating by sheep. This could involve identifying the proportion of sheep in different aged flocks that may lack the physiological plasticity enabling other individuals to consume ragwort. The greater toxicity of ragwort to lambs compared with ewes suggests that sheep may not develop a stable pattern of ragwort ingestion until they can eat it 'safely'. Perhaps a greater preference for ragwort could be induced if lambs were denied access to the plant until they were old enough to detoxify the alkaloids effectively. Poole and Cairns (1940) reported that sheep from "non-ragwort country" developed a clear "preference" for the plant "once they had acquired a taste for it". A comparison between adult ewes that have never experienced ragwort, with a group retained on ragwort-containing pasture since birth, could be used to investigate this possibility.

3.5.6. ***Ragwort feeding of ewes*** The ewes that had returned from a ragwort-free environment, where they were kept from lambing to weaning, were observed eating ragwort four times as often as their non-deprived counterparts during Weeks 1 and 3. Random allocation to background pasture treatment and a similar procedure for choosing ragwort-eaters did not result in similar ragwort preferences between each ewe group. This may have been because sheep food preferences are flexible, and can be modified by recent diet (Newman *et al.*, 1992; Parsons *et al.*, 1994). Sheep often prefer pasture species different to those grazed most recently (Newman *et al.*, 1992), although this preference disappears over time (Parsons *et al.*, 1994). In the case of the ewes deprived of ragwort from lambing until weaning, increased ragwort-eating following reintroduction to ragwort-dense pasture may indicate a short-lived preference for a familiar food type different from those most recently encountered. It is not known what effect this differential ragwort eating by the two ewe groups may have had on the lambs that they grazed with. One possibility is that the ewe group that grazed more ragwort provided the lambs that grazed with them with increased opportunities to co-act in ragwort grazing. However, the possible effect of differential social facilitation may not be directly proportional to the ragwort-grazing of the ewes.

In future studies, the ewes should be removed before lamb behavior is sampled, to avoid the potential problems of differential social facilitation, and inseparable consumption of ragwort.

What about carry-over of 'avid ewes', when scanning is done?

3.5.7. ***Ragwort growth stage preferences of lambs*** During Week 12, the lambs from ragwort-free pastures consumed a much greater proportion of rosette volume than the lambs from ragwort-present pasture. Walker *et al.* (1992) found a similar preference in naive lambs for the vegetative phase of leafy spurge compared with no phenological stage preference among exposed lambs. The exposed lambs had been fed mostly on flowering leafy spurge plants during rearing, and it was thought that this may have caused the difference. For the present experiment, ragwort was not flowering when the ragwort-present lambs were born. Thus the lambs from both pasture backgrounds initially experienced elongated plants at about the same time. Further, there was no difference in elongated plant reduction by the lambs from each background.

The proportion values used for volume reduction could be deceptive if the average rosette plant has less biomass than the average elongated plant. Thus, equal proportions of rosette and elongated plants removed by grazing could indicate that more elongated plant material was grazed in total. The total weight of rosette vs elongated material consumed will be needed to generate reliable estimates of any phenological stage preferences between the lambs from the two background pasture types.

3.5.8. ***Activity budgets of ewes and lambs*** Hungry sheep spend more time grazing than those that are not hungry (Newman *et al.*, 1994). During 24-hours of confinement the sheep may have consumed most of the forage from the grazing area which may have increased time spent grazing during the initial hour on fresh pasture. The mean proportion of time spent grazing (ragwort + pasture) for the ewes of 72% was similar to that found by Ballance (1985) for Campbell Island feral sheep of 70.2%. This suggests that the grazing time of sheep after restricted grazing for 24-hrs may be similar to *ad libitum* grazing, possibly because there was enough forage in each daily grazing area for the sheep to avoid fasting.

Lambs spent more total time grazing (ragwort + pasture) during Week 12 than the ewes that grazed with them did during Weeks 1 and 3. This may reflect the greater growth requirement of the lambs (Provenza, 1995).

3.5.9. ***Conclusions*** Lambs may graze very little ragwort immediately following weaning, regardless of background pasture type. Although pre-weaning exposure to ragwort and post-weaning grazing with ewes increased ragwort eating by lambs in the short-term, both interventions failed to generate heightened grazing of ragwort in the long-term. From a practical perspective, freshly weaned lambs may not provide immediate ragwort control, although their ragwort-grazing will probably increase within 12 Weeks. Also, farmers may not need to ensure that lambs destined for ragwort-control experience ragwort-containing pastures before weaning, because simply confining lambs to such pastures immediately after weaning may have a similar effect on subsequent ragwort grazing.

Chapter Four

General Discussion

4.1. Summary of main findings

The ragwort grazing behaviour of different aged sheep was studied during *ad libitum* grazing, restricted outdoor grazing, and indoor acceptance tests. More observations were made for lambs than for mature ewes or hoggets. Working with lambs provided an opportunity to observe how ragwort feeding might initially develop and how it may change with increasing age and experience. The grazing activities of the lambs were controlled from birth, whereas the grazing history of the hoggets and mature ewes, apart from the general information that they were exposed to ragwort previously, was largely unknown.

Ragwort feeding by lambs reared on either ragwort-containing or ragwort-free pasture was studied (Chapter 3). The results suggested that exposing lambs to ragwort before weaning increased their consumption of ragwort immediately after weaning. Ragwort-eating by lambs without previous ragwort exposure was facilitated by the presence of mature ewes confined with them. By the fourteenth week after weaning, a combination of increased age and cumulative grazing experiences had eclipsed any past effect of pre-weaning grazing or the presence of a 'teacher'. However, these were group effects, and irrespective of grazing background or ewe presence, some lambs spent more time eating ragwort than others. The lambs with the strongest ragwort preferences or aversions were classed as either avid- or averse-ragwort eaters and then studied along with similarly classified hoggets and mature ewes.

Regardless of age, sheep classed as avid-eaters ate more ragwort and consumed it more readily than those classed as ragwort-averse (Chapter ~~two~~ 2). These differences in feeding behaviour did not change during a one-month period when all individuals were compelled to eat ragwort. All sheep were found to accept ragwort if other food was absent, but when given the opportunity to choose, ragwort-averse sheep grazed something other than ragwort.

Some of the lambs identified during the fourteenth week after weaning as ragwort-averse, did not retain this ragwort avoidance after a year of grazing ragwort pastures. This may indicate the development of an increased tolerance to ragwort toxins or simply an acquired preference for ragwort during the interim period (Section 4.3.2.).

4.2. Implications for farmers

4.2.1. ***Selecting the best sheep for ragwort control*** Some sheep eat more ragwort than others. These avid ragwort eaters may be easily identified from other flock members because they often selectively graze ragwort material as soon as they are introduced onto fresh, ragwort-containing pasture. Fewer sheep may be needed for ragwort control if only avid ragwort eaters are used.

4.2.2. ***Ragwort averse sheep*** These sheep will graze ragwort if they are confined on an infestation long enough. However, they may overgraze the pasture before switching to ragwort. Overgrazing by sheep may create holes in the grass sward which suit ragwort colonisation (Watt, 1987a). The ragwort grazing behaviour of ragwort averse sheep is not easily modified, so, if present, these individuals should be removed from ragwort control flocks. Before buying sheep for ragwort control some evidence from the vendor that the sheep graze ragwort may be an essential requirement before completing the purchase.

4.2.3. ***Ragwort control with lambs*** Mortimer and White (1975) suggested that lambs destined for early slaughter be used to control ragwort to prevent the poisoning of breeding ewes. However, young lambs may graze very little ragwort until at least five weeks after weaning. Ragwort grazing by lambs does increase between five and 14 weeks following weaning, although the nature and timing of the increase within this period is not known. Lambs may only graze the leaves of ragwort plants, whereas mature ewes graze the crown (Cameron, 1935). This feeding practice of ewes results in higher plant mortality. Thus a cull flock of old ewes may be more effective at controlling ragwort than lambs.

4.3. Future Work

4.3.1. *Replication* The present study suggests that some Romney sheep at Ballantrae Research Station avoid eating ragwort during *ad libitum* grazing. This agrees with a previous study of a Romney flock at Ballantrae (Betteridge *et al.*, 1994). However, each study used a separate definition of 'ragwort-averse' and so are not directly comparable. Further, both studies were not replicated so the reliability of the ragwort-averse sheep proportions suggested by each is unknown. A standardised procedure for identifying ragwort-averse sheep will need to be used to observe a number of flocks so that reliable estimates can be determined.

Only anecdotal information exists on whether ragwort-averse Romney sheep are common on farms other than Ballantrae. It is also not known if other sheep breeds contain ragwort-averse individuals, although Betteridge *et al.* (1994) found that mixed age Merino wethers gave very poor ragwort control.

4.3.2. *Differences in the consumption of ragwort by sheep* Ragwort grazing behaviour may vary among sheep because some may have had more ragwort eating experiences during a sensitive period for diet learning than others. With increasing age, sheep become more resistant to eating novel foods (Chapple and Lynch, 1986). Therefore, sheep with apparent ragwort aversions may simply have not sampled ragwort early in life, and as a consequence avoided it later because of its relative novelty. However, when ragwort-averse sheep were compelled to eat ragwort, this experience did not modify their ragwort grazing during the following month. For lambs also, a lack of ragwort experience may not explain apparent ragwort aversions, because these were not related to pre-weaning grazing experiences on ragwort-containing or ragwort-absent pasture.

Apart from a lack of experience, some sheep may avoid ragwort because eating it has a negative effect on them. Provenza *et al.* (1992) suggested that sheep are able to make associations between the taste of food and any positive or negative effects that result from eating it. These associations are strongest when the effects of eating a food (eg malaise) occur soon after its ingestion (Provenza, 1995). The detrimental effects of ingesting ragwort are usually not immediate, and this may prevent sheep from making an association between eating ragwort and resulting illnesses (Provenza, 1995). This suggests that few sheep would be expected to avoid ragwort because ~~if~~ of its toxic effects. However, sheep vary in their ability to process phytotoxins and some are hypersensitive to specific types (Provenza *et al.*, 1992). This may apply to the pyrrolizidine alkaloids in ragwort. For example, Mortimer and White (1975) fed 100 grams of dried ragwort leaves to four sheep over a 20 week period. One of the sheep died after 11 weeks, the next after 18 weeks and a third after 46 weeks; 26 weeks after the cessation of dosing. The fourth sheep showed little effect of toxicosis when slaughtered 18 months later. These differences in the ability of sheep to tolerate plant toxins may help to explain differences in diet selection among individuals (Provenza *et al.*, 1992). Therefore, sheep that are less tolerant to pyrrolizidine alkaloids may experience more immediate negative effects following ragwort ingestion, and may form ragwort aversions associated with them.

To avoid eating a plant that has negative post-ingestive consequences, sheep must be able to identify the plant accurately (Provenza, 1995). Sheep display a strong sensitivity to bitter tasting substances and this may help them to identify and avoid plants that contain alkaloids (Chapple and Lynch, 1986). Ragwort tastes bitter to sheep, although the pyrrolizidine alkaloids in their pure form do not (Molyneux and Ralphs, 1992). The present study found that lambs often remove ragwort leaves from a plant without eating them. This may indicate that some lambs use taste associations to avoid eating ragwort. Ragwort may become more palatable to sheep after being sprayed with phenoxy herbicide (Popay and Field, 1996). Perhaps this increase in palatability results from masking the taste cues that ragwort-averse individuals may use to avoid grazing ragwort. Future studies with ragwort-averse sheep will be needed to investigate this possibility.

Ragwort-averse sheep will eat ragwort indoors if no other feed is unavailable. Blood enzyme tests are available to determine the relative levels of toxin accumulation from ragwort grazing (Bedell *et al.*, 1981). Following indoor trials, a comparison of test results between avid and averse ragwort eaters may determine whether ragwort-averse sheep are more easily poisoned.

Unborn lambs may be able to associate food flavours with negative effects experienced while in utero (Provenza *et al.*, 1992). This suggests that some lambs may develop ragwort aversions before they are born. It is possible that all the lambs used in the present study experienced ragwort before being born, because the ewes that reared lambs on ragwort-free pasture may have grazed ragwort until two weeks before giving birth. Thus, future studies of lambs that have had no opportunities to sample ragwort will require moving ewes from ragwort-present pasture to ragwort-absent pasture before being inseminated.

The pyrroloizidine alkaloids in ragwort are more toxic to lambs than mature sheep (Cameron, 1935). Therefore, lambs may be expected to eat less ragwort because they may experience relatively immediate negative effects of ingestion. In the present study, lambs initially grazed less ragwort than mature ewes, however this may be confounded by the greater ragwort grazing experience of the ewes. Future work will involve separating the relative effects of experience and physiology on the *ad libitum* ingestion of ragwort by lambs and ewes. This may not be simple. Even if ewes and lambs are first introduced to ragwort at the same time, a tendency for lambs to graze novel food more readily than ewes may confound results.

4.3.3. ***Stocking rates for ragwort control with sheep*** Betteridge *et al.* (1994) attempted to quantify the minimum number of sheep stock units/ha required to control a ragwort infestation, but the presence of sheep reluctant to graze ragwort made this task difficult. By only using sheep that display avid ragwort-eating, a more reliable stocking rate for ragwort control may be calculable.

4.3.4. ***Integrating sheep with other ragwort control measures*** Farmers rarely depend on a single method for ragwort control because varying infestation attributes can demand different ragwort control solutions (Bedell, *et al.*, 1981). Judicious timing of sheep-grazing integrated with other ragwort management practices may provide better ragwort control than with sheep alone (Popay and Field, 1996). An example is using sheep to control ragwort after spraying it with herbicides (Bedell *et al.*, 1981). More research into the effects of combining sheep grazing with insect biological control is also required (Popay and Field, 1996).

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Appendix A: Paper Submitted to the Journal of Range Management.

Can the Rearing Conditions for Lambs Increase Tansy Ragwort Grazing?

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Keywords: *Senecio jacobaea*, lambs, grazing, training, social facilitation

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Abstract

Grazing by sheep is an accepted method of controlling tansy ragwort (*Senecio jacobaea*), but some flock members seldom eat it. Our objectives were to determine if pre-weaning exposure to tansy ragwort increases later consumption of the plant by lambs, and if confinement with ragwort-eating "teacher" ewes after weaning facilitates ragwort eating. The sampling periods were Weeks 1, 3, and 12 following weaning. During each period grazing behavior was observed for 1-hour each day and the 24-hour reduction in ragwort volume measured on each of 4 or 5 consecutive days. Lambs exposed to ragwort before weaning removed more ragwort from confinement plots than non-exposed lambs during the first two sampling periods ($P < 0.05$). Lambs that grazed with ewes ate ragwort more frequently during direct observation, than lambs without ewes during Weeks 1 and 3 ($P < 0.05$). Of the lambs that grazed with ewes, those reared on ragwort-containing pasture ate ragwort more frequently than non-exposed lambs ($P < 0.05$), but their ewes also ate ragwort more frequently than the opposing ewe group ($P < 0.05$). Although the grazing management techniques employed initially increased ragwort-eating by lambs, the observed effects did not persist into the 12th week following weaning. Lambs in all groups increased their ragwort eating markedly, as indicated by both measurements, between Weeks 3 and 12. This may indicate an increased ability of lambs to consume ragwort with increasing age. Behavioral interventions aimed at increasing the consumption of weeds by lambs may need to take into account possible age-related differences in the plant toxin tolerances of sheep. Grazing management techniques employed before, and immediately after weaning, appear not to effect the later ragwort-eating of lambs.

Introduction

Tansy ragwort (*Senecio jacobaea*) is a biennial, broadleaf weed of cattle pasture found in Europe, North Western areas of the United States, New Zealand, and elsewhere (Wardle 1987). Cattle and horses tend to avoid grazing ragwort which contains pyrrolizidine alkaloids that are highly toxic to them (Cheeke 1994). Despite this natural avoidance, accidental or forced ingestion can occur, and stock losses often result (Sharrow and Mosher 1982). Grazing by sheep is an effective ragwort-control method (Poole and Cairns 1940; Sharrow and Mosher 1982; Amor et al. 1983; Betteridge et al. 1994). Unlike cattle, sheep can tolerate, and often readily include, large amounts (up to 50%) of ragwort in their diet (Cheeke 1994).

In New Zealand, a trend towards all-cattle farming has seen the subsequent removal of sheep from previously integrated sheep and cattle systems. This has resulted in dense stands of ragwort in areas where previously it was not a problem (Betteridge et al. 1994). Re-introducing a minimum number of sheep to control ragwort infestations could be a suitable compromise (Betteridge et al. 1994). However, quantifying the minimum number of sheep relies on all individuals having similar ragwort-eating behaviour. In practice this appears not to be the case and a small proportion of sheep may avoid eating ragwort altogether (Betteridge et al. 1994).

The grazing experiences of lambs during weaning influence their food preferences as adult sheep (Ramos and Tennessen 1992, Walker et al. 1992). Grazing with mothers (Nolte et al. 1990), older sheep (Chapple and Lynch 1986), or conspecifics (Scott et al. 1996), can also modify food preferences of lambs.

The objectives of the present study were to examine the effect of pre-weaning ragwort exposure on the subsequent grazing of ragwort by lambs; to see if the presence of older, ragwort-eating ewes ("teachers") would modify this activity; and to assess the usefulness of any induced behavioral differences in improving ragwort biological control by sheep.

Materials and Methods

The experiment ran over three months on hill country farmland at the AgResearch Ballantrae research station (36°S) near Palmerston North, New Zealand.

Pre-trial

Thirty pregnant Romney ewes were randomly selected from a Ballantrae flock and transported to pasture free of ragwort in mid-August (early spring) 1995. A second group of 30 ewes selected from the same flock was left to graze on ragwort-containing pasture at Ballantrae. Lambing began in early September, and lambs were reared with their mothers on their respective pasture types.

On 14 November 1995 the ewes and lambs on ragwort-free pasture were returned to Ballantrae and retained on pasture cleared of ragwort. Twenty-four hours later lambs in both groups were weaned, with the selected ewes being run with the lambs from the opposing group. The lamb groups sourced from both ragwort-containing and ragwort-free pastures were split into two sub-groups using a weight-restricted randomisation with the 15 heaviest lambs from each of the four sub-groups being used. All lambs were identified according to source, with a large red number on each shoulder, side, and rump. This produced four distinct groups identifiable through tag and number colour combination. During the experiment one group of lambs sourced from ragwort-containing pasture was confined with six confirmed ragwort-eating ewes that had not eaten ragwort from lambing, and one group of lambs sourced from ragwort-free pasture with six ewes with no recent ragwort restriction. The two remaining lamb groups grazed without ewes.

The lambs born on ragwort-free pasture were retained on similar pasture for two weeks at Ballantrae, prior to starting the trial on 27 November 1995.

Trial Design

Four 10-m wide pasture lanes were created with electric sheep netting in a paddock infested with ragwort. Care was taken to ensure that ragwort content and size distribution both between and within lanes was similar. Within these lanes, daily "breaks" of pasture were offered from 0900 or 1030, sufficient for 24-hour feeding to provide moderate animal growth, but less than *ad libitum* feeding. Lambs with ewes present were given larger allowances than lambs grazed alone. Sheep were introduced to the new break immediately prior to observational recording.

Plant measurements and animal observations were made during three separate observation periods; Week 1 (immediately following weaning), Week 3, and Week 12. Five days of observation were made during Week 1, and four days of consecutive observation were made during Weeks 3 and 12. The ewes were removed from their respective lamb groups immediately prior to the first observation day of Week 12. All four groups were grazed separately from Week 1 through to Week 12.

Animal Measurements

At 0900 two observers scan-sampled (Altmann 1974) 15 lambs at two-minute intervals. During a scan each individual was categorised as eating ragwort, eating a plant other than ragwort, or not eating. These scan observations lasted for one hour and were repeated for the second group of animals at 1030. A third observer recorded the same activities for the ewes in each of these groups.

Plant Measurements

Within each daily break, 20 ragwort plants were identified with a numbered peg, and the height and two width dimensions at ground level (taken at right-angles to each other) were recorded. Plant volumes were estimated on the assumption that the plants were cylindrical in shape and that reduction in volume equated to ragwort consumption. These measurements were repeated once animals were removed from the plot after 24 hours of confinement.

Analysis

Statistical analyses were conducted using the GLM procedures of SAS, and all means and standard errors quoted refer to least squares means and their standard errors (SAS Institute 1990). Probability levels of $P < 0.05$ constituted statistical significance.

Results

The mean ragwort plant heights measured during Weeks 1, 3, and 12, were 25, 29, and 48-cm respectively; and the mean volumes were 0.26, 0.22, and 0.29-m^3. The ragwort heights and volumes were similar between lanes within each week (week × group interaction; $P = 0.35$). Mean grass height, before grazing, was 16, 13, and 11-cm (3100-2100 kg of Dry-Matter per ha) in each period respectively, and the 24-hour post-grazing height reduction was always between 46 and 48%. The average weaning weight of the lambs was 20-kg and this increased to 29.7-kg at the conclusion of Week 12.

For both lamb groups confined without ewes, the mean percentage of ragwort-feeding-scans increased from 0.4% during Weeks 1 and 3, to 6.5% during Week 12 ($P < 0.05$). The mean percentage of ragwort removed from the plots after 24-hours increased from Week 1 to 3, from 16 to 30%, and then to 60% during Week 12 ($P < 0.05$), for the same two groups.

During the first hour of confinement in fresh pasture in Weeks 1 and 3, both lamb groups without ewes grazed ragwort with a similar frequency ($P = 0.10$). However, the lambs reared on ragwort-containing pasture removed more ragwort on a daily basis (33% of original volume), than the lambs reared on ragwort-absent pasture (13%), averaged over both weeks (Table 1).

Lambs confined with ewes during Weeks 1 and 3 ate ragwort more frequently during the first hour of grazing than the groups with no adults present ($P < 0.05$). A comparison of daily ragwort consumption by the lambs in these groups was not possible because of the inseparable contributions of ewes and lambs to the removal of ragwort from the plots. Of the lambs confined with ewes during Weeks 1 and 3, those reared on ragwort-containing pasture ate ragwort during the first hour of grazing more frequently than the lambs reared on pasture with no ragwort ($P < 0.05$) (Table 2). However, the ewes that grazed with them displayed a similar pattern; as ewes confined with ragwort-reared lambs ate ragwort more often (16%) than ewes confined with lambs reared without access to ragwort (5%; $P < 0.05$), averaged over both weeks (Table 2). Ragwort-eating during the first hour of grazing increased in frequency from Week 1 to Week 3 for the lambs with ewes present (Table 2). This main effect of Week did not occur for the lambs without ewes (Table 1).

When all four lamb groups grazed alone during Week 12 there was no effect of either rearing condition or ewe presence (up to the start of week 12) on ragwort eating behavior, with respect to both the 1-hour scan and 24-hour volume reduction measurements (Table 3). There was also no interaction between rearing condition and ewe presence (Table 3), as measured by both 1-hour scan-sampling ($P = 0.91$), and 24-hour ragwort volume reduction ($P = 0.12$).

Discussion

Ragwort Exposure

Lambs reared to weaning on ragwort-containing pasture removed more ragwort per day during the first and third weeks after weaning than lambs reared without exposure to ragwort. This difference was not detected during the single hour of visual scan observations made of the lambs each day. This finding, that short-term observations of grazing behaviour, made at a single time of day, were not representative of longer-term grazing patterns has also been found by Parsons et al. (1994).

The measured difference in ragwort utilisation by the lambs from each pasture background supports an unmeasured assumption of the present research; that the lambs reared on ragwort-containing-pasture actually did sample ragwort prior to weaning. This is important because previous research suggests that simply exposing lambs to a new food has little effect on later food preferences, unless sampling of the food occurs (Chapple and Lynch 1986). Substantial reduction in ragwort volume clearly occurred in the ragwort-containing-paddocks occupied by the ewes and their lambs before weaning occurred (J.Napier pers. comm.). This would have produced an environment where the lambs had many opportunities to interact with ewes eating ragwort. This lends further support to the assumption that the unweaned lambs experienced ragwort during their exposure to it. Participating with a grazing mother has an even greater influence on the later food preferences of unweaned lambs than learning through trial and error alone (Thorhallsdottir et al. 1990a), and probably contributed to the greater removal of ragwort by the ragwort-exposed lambs during Weeks 1 and 3.

If the percentage of feeding scans in which ragwort was the food being eaten is assumed to be proportional to the volume of ragwort removed from the pasture, then the lambs reared on ragwort-containing pasture only ate more ragwort than the non-exposed lambs after the daily sessions of direct observation by researchers. Ragwort may not have been a preferred food for these lambs, and therefore remained relatively untouched until more preferred species were depleted, and/or rendered inedible through trampling. A second possibility is that ragwort was not preferred by ragwort-exposed lambs in the morning, but was taken at some time later in the day. This type of regular diurnal preference pattern, for reasons other than the depletion of a previously preferred species, could indicate a determined strategy of ingestion (Sibley 1981). Both possibilities are equally likely, and distinguishing between them would involve observing lambs grazing on large areas of pasture, to ensure the maintenance of free-choice grazing throughout each 24-hour period of confinement (Parsons et al. 1994). Further, both possibilities require the ragwort-exposed lambs to have sampled ragwort before weaning, and to have developed a learned response that persisted after weaning in a familiar grazing environment (Scott et al. 1996). In contrast, lambs reared on ragwort-free-pasture probably grazed only familiar species when first exposed to ragwort (a novel plant) in an environment that was initially unfamiliar to them (Scott et al. 1996); and ragwort remained relatively untouched as a consequence.

Social Facilitation

Social facilitation occurs when a learned behaviour is performed at a greater rate when animals co-act with other individuals, than when the behaviour is emitted in the absence of others (Thorhallsdottir et al. 1990b). During Weeks 1 and 3, the presence of ewes facilitated the sampling of ragwort by lambs from both grazing backgrounds, during the first hour of fresh pasture confinement. The relative contributions of social facilitation and persistent learned preferences to the increased eating of ragwort are inseparable, because the lambs always grazed with the ewes during Weeks 1 and 3. It is therefore unknown whether the increased level of ragwort sampling by the lambs would have persisted in the absence of the ewes. During Week 12, when all lamb groups grazed alone, those that had grazed with ewes during the previous 11 weeks no longer ate ragwort more frequently than those that had not. There was also no difference in the Week 12 percentage of ragwort volume removed over 24-hours by any of the groups, suggesting that ewes may have initially facilitated the eating of ragwort by lambs without increasing its long-term inclusion in their diet. Certainly, the greater incidence of ragwort sampling in Week 1 by the lambs that were reared on ragwort-free pasture and confined with ewes, compared with their counterparts that grazed without ewes, suggests that the ewes may have been instrumental in facilitating their initial consumption of ragwort. Also, both of the lamb groups with ewes present ate ragwort more frequently in Week 3 than in Week 1 without a corresponding increase in ragwort-eating by their respective ewes. This suggests that a change in feeding behavior by the lambs, rather than an increase in social facilitation through the ewes, had occurred. The incidence of ragwort eating by the lamb groups that grazed without ewes was the same during Weeks 1 and 3; this further supports the possibility that the ewes were the cause of the increased Week 3 ragwort sampling displayed by the lambs that they grazed with.

Of the two lamb groups that grazed with ewes, the lambs reared on ragwort-containing pasture ate ragwort more frequently during the first hour of grazing than the lambs sourced from ragwort-free pasture. Although this could simply reflect the differing pre-weaning ragwort experiences of the two groups, it may also indicate a difference in the effectiveness of the ewe "teachers" assigned to them. Interestingly, the ewes that had returned from a ragwort-free environment, where they were kept from lambing to weaning, were observed eating ragwort four times as often as their non-deprived counterparts during Weeks 1 and 3. Thus, the ragwort-exposed-lambs which ate ragwort more often than the non-exposed lambs, did so in the presence of ewes that also ate ragwort more often than the ewes that grazed with the non-exposed lambs. This suggests that the ragwort-exposed lambs may have grazed more ragwort because of increased opportunities to co-act with ragwort-grazing ewes, rather than because of their pre-weaning ragwort exposure. Again, the reliability of sampling periods is an issue, because this 1-hour pattern may not represent grazing patterns that persist throughout an entire day. However, a 24-hour comparison of ragwort removal was not possible because of the inseparable contributions made by lambs and ewes. In future studies, the ewes should be removed before lamb behavior is sampled, to avoid the problems of differential social facilitation, and inseparable consumption of ragwort.

Random allocation to treatment did not result in similar ragwort preferences between each ewe group. This may have been because sheep food preferences are flexible, and can be modified by recent diet (Newman et al. 1992; Parsons et al. 1994). Sheep often prefer pasture species different to those grazed most recently (Newman et al. 1992), although this preference disappears over time (Parsons et al. 1994). In the case of the ewes deprived of ragwort from lambing until weaning, increased ragwort-eating following reintroduction to ragwort-dense pasture may indicate a short-lived preference for a familiar food type different from those most recently encountered. It is unknown whether this increased ragwort eating continued beyond the first hour of grazing by the ewes on fresh ragwort-containing pasture.

Persistence of Training

Ragwort-eating, in comparison to other feeding, increased substantially between Weeks 3 and 12 for all four lamb groups. This pattern of initial low intake of a food type by lambs, followed by a large increase in consumption is a regularly reported finding; eg Chapple and Lynch (1986) with wheat; and Ralph et al. (1990) and Pfister & Price (1996) with locoweed, a plant, which like ragwort also contains toxic alkaloids. The gradual process of habituation to a novel food is one possible interpretation of the increase (Ralphs et al. 1990). This, however, fails to explain why lambs exposed to ragwort from birth underwent an increase similar in magnitude to the lambs that remained unexposed until after weaning. Because of the data gap between weeks 3 and 12 we do not know: when the marked increase in ragwort-eating during this period occurred; whether the transition was sudden or gradual; and whether the pattern was the same for each group. However, the lack of any differences between all four lamb groups during Week 12, regardless of rearing conditions or experiences with ewes, suggests that perhaps the age of the lambs was the largest determinant of the amount of ragwort included in the diet.

Young animals are generally more susceptible to ragwort pyrrolizidine alkaloid (PA) toxicosis than older ones, because of increased cellular activity and higher levels of PA bioactivating enzymes in the liver (Johnson et al. 1985). Furthermore, lambs are more susceptible than older sheep to the toxic effects of excess ragwort ingestion (Olson and Lacey 1994; Cameron 1935, cited in Wardle 1987). Possibly the lambs used in the present study developed an increased tolerance for PAs between Weeks 3 and 12 that enabled them to eat more ragwort. This could have occurred through a decline in PA bioactivating enzymes and/or an increase in PA detoxifying enzymes in the liver (Cheeke 1994).

Physiological changes that allow the ingestion of toxic foods may not only occur as a result of developmental processes; but may also occur as an adaptive response to a major change in forage type (Olson and Lacey 1994). Such adaptations could involve changes in rumen microflora and/or the relative concentrations of enzymes in the liver (Olson and Lacey 1994). This may help to explain the observation by Poole and Cairns (1940) that adult sheep with no ragwort experience tend to eat very little of the plant initially (unless forced to eat it through a lack of alternative forage) until, after continued sampling, a taste for the plant rapidly develops; and it eventually becomes a large component of the diet.

Clearly, further research should aim to separate the relative effects of age, physiology, and learning, on the level of ragwort-eating by sheep. This will involve identifying the proportion of sheep in different aged flocks that lack the physiological plasticity enabling other individuals to consume ragwort. The greater toxicity of ragwort to lambs compared with ewes suggests that sheep may not develop a stable pattern of ragwort ingestion until they can eat it "safely". Perhaps a greater preference for ragwort could be induced if lambs were denied access to the plant until they were old enough to detoxify the alkaloids effectively. Poole and Cairns (1940) reported that sheep from "non-ragwort country" developed a clear "preference" for the plant "once they had acquired a taste for it". A comparison between adult ewes that have never experienced ragwort, with a group retained on ragwort-containing pasture since birth, could be used to investigate this possibility.

Conclusions

Although pre-weaning exposure to ragwort and post-weaning grazing with ewes increased ragwort eating by lambs in the short-term, both interventions failed to generate heightened grazing of ragwort in the long-term. Behavioural interventions aimed at increasing the consumption of weeds by lambs, as a means of weed control, may need to take into account apparent age-related differences in toxin tolerances. From a practical perspective, farmers need not ensure that lambs destined for ragwort-control experience ragwort-containing pastures before weaning, because simply confining lambs to such pastures immediately after weaning has the same effect on subsequent ragwort grazing.

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Table 1. Mean (± standard error) percentage of feeding scans spent eating ragwort during the first hour on new pasture over 5 days (Week 1) and 4 days (Week 3), and mean daily volume (%) of ragwort removed over 24-hour grazing periods during Weeks 1 and 3 by lambs without ewes and reared to weaning on ragwort-containing (Exposed) and ragwort-free pastures (Naive).

Rearing experience (Origin)	Ragwort eating (%)	Ragwort removal (%)
Week 1		
Exposed	0.76 ± 0.24	27 ± 6
Naive	0.05 ± 0.24	4 ± 6
Week 3		
Exposed	0.54 ± 0.27	39 ± 6
Naive	0.30 ± 0.27	21 ± 6
Probability > F		
Origin	0.099	0.024
Week	0.952	0.080
Origin x Week	0.387	0.720

Table 2. Mean (± standard error) percentage of feeding scans spent eating ragwort during the first hour on new pasture over 5 days (Week 1) and 4 days (Week 3), by lambs reared to weaning on ragwort-containing (Exposed) and ragwort-free (Naive) pastures and also by the ewes that grazed with them during Weeks 1 and 3.

Rearing experience of lambs (Origin)	Lamb ragwort grazing (%)	Ewe ragwort grazing (%)
Week 1		
Exposed	0.8 ± 0.3	20 ± 4
Naive	0.5 ± 0.3	4 ± 4
Week 3		
Exposed	2.5 ± 0.3	12 ± 4
Naive	1.2 ± 0.3	6 ± 4
Probability > F		
Origin	0.040	0.022
Week	0.005	0.465
Origin x Week	0.174	0.184

Table 3. Mean (± standard error) percentage of feeding scans spent eating ragwort during the first hour on new pasture, and mean daily volume (%) of ragwort removed over 24-hour grazing periods during Week 12, by lambs reared to weaning on ragwort-containing (Exposed) and ragwort-free (Naive) pastures and grazed after weaning with and without ewes.

Rearing experience (Origin)	Ragwort eating (%)	Ragwort removal (%)
Ewes Present		
Exposed	7 ± 2	51 ± 4
Naive	8 ± 2	65 ± 4
Ewes Absent		
Exposed	6 ± 2	61 ± 4
Naive	7 ± 2	60 ± 4
Probability > F		
Origin	0.667	0.166
Ewe	0.611	0.589
Origin x Ewe	0.913	0.122