RELATIONSHIP BETWEEN FLOCKING, DIET AND MORPHOLOGY IN WOODPIGEONS (*COLUMBA PALUMBUS*) DURING EARLY AUTUMN IN SOUTH-EASTERN NORWAY

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Abstract

Woodpigeon (*Columba palumbus*) diet in Norway has not been thoroughly examined, in addition crop preference of wild woodpigeons in combination with flock behaviour has been insufficiently investigated. I studied flock behaviour, diet, crop preference and morphological characters in woodpigeon during late summer and early autumn in south eastern Norway, based on a total of 121 woodpigeons shot. Only half of the woodpigeons in flocks had eaten, compared to four of five of those woodpigeons flying in pairs at the moment they were shot. My findings indicate that woodpigeons have to gain a certain body weight before they moult for the first time and obtain their white neck band. Of 82 woodpigeons that had one or several objects in their crop, 72 were examined in detail. The most frequently found food item was wheat. Peas were the most preferred in proportion to availability and oat the least preferred. Of the woodpigeons shot on pea, wheat or barley fields; the ones shot on pea fields had the highest mean dry weight eaten fodder, the ones shot on wheat fields had the highest portion of woodpigeons that had eaten, whereas woodpigeons shot on barley fields had both least mean dry weight eaten fodder and lowest portion of woodpigeons that had eaten, respectively. The probability that a woodpigeon had eaten when it were shot increased with its net weight.

Keywords. Woodpigeon (*Columba palumbus*); diet; morphologic measurements; flock behaviour; crop preference

Sammendrag

Ringduas (*Columba palumbus*) diett er lite studert i Norge, i tillegg er avlingspreferanse hos ville ringduer i kombinasjon med flokk atferd dårlig undersøkt. Jeg undersøkte flokkatferd, diet, avlingspreferanse og morfologiske trekk hos ringdue ved slutten av sommeren og starten på høsten i Sørøst-Norge, basert på et totalt antall bestående av 121 ringduer skutt. Kun halvparten av ringduene i flokk hadde spist, sammenlignet med fire av fem av ringduene som fløy i par det øyeblikket de ble skutt. Mine funn indikerer at ringduene må oppnå en viss kroppsvekt før de myter for første gang og får sine karakteristiske hvite nakkeflekker. Av de 82 ringduene som hadde ett eller flere objekter i kroposen ble 72 undersøk i detalj. Det mest vanlig observerte matslaget var hvete. Erter var høyest preferert i forhold til tilgjengeligheten, og havre var den minst prefererte. Av de ringduene som ble skutt på enten erte-, hvete- eller byggåkrer; hadde de som ble skutt på erteåkrer høyest gjennomsnitt av vekt på spist (tørka) fôr, de som ble skutt på hveteåkrer hadde høyest gjennomsnitt av ringduer som allerede hadde spist, mens derimot ringduer skutt på byggåkrer hadde både lavest gjennomsnitt av vekt på spist (tørka) fôr og lavest andel ringduer som allerede hadde spist. Sannsynligheten for at en ringdue hadde spist når den ble skutt økte med nettovekten på ringduen.

Nøkkelord. Ringdue (*Columba palumbus*); diet; morfologiske mål; flokk atferd; avlings preferanse.

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Introduction

Flocking behaviour is common in birds feeding on the ground. There are two main advantages of being in a flock. The first is that the chance of being caught by a predator decreases as the flock size increases (Kenward 1978). The most important reason is the vigilance effect; the larger the flocks, the more individuals can spot an approaching predator (Lima 1990). In addition, the predator get more confused when there are several prey individuals to choose between (Kenward 1978). The other advantage of being in a flock is that individuals can use other flock members to locate suitable food sources (Lockie 1956b, Murton and Isaacson 1962, Murton 1971b, Sonerud et al. 2001).

Flock behavior in relation to foraging has been studied in many birds e.g.: various corvids Corvidae (Lockie 1956a, 1956b, Saino 1994, Sonerud et al. 2001), woodpeckers Picidae (Sullivan 1984), cockatoos Cacatuidae (Cameron 2005), storks Ciconiidae (Alonso et al. 1994), waders Scolopacidae (Beauchamp 2005), rheas *Rhea* (Reboreda and Fernandez 1997), various finches Fringillidae (Gluck 1986, Beveridge and Deag 1987, Gluck 1987, Benkman 1988), sparrows Passeridae (Barnard 1980, Beveridge and Deag 1987), starlings Sturnidae (Beveridge and Deag 1987, Fernandez-Juricic et al. 2004, Fernandez-Juricic et al. 2005) and also in various pigeons Columbidae (Murton and Isaacson 1962, Murton et al. 1971, Lefebvre et al. 1996, Robichaud et al. 1996, Hatch and Lefebvre 1997, Sadedin and Elgar 1998).

The woodpigeon (*Columba palumbus*) i.e. the largest pigeon in Europe; (Haftorn 1971, Svensson et al. 1999). It is a common bird (Goodwin 1977) which has expanded its range from the 19^{th} century or earlier (Cramp 1985). The breeding population in Norway is estimated to 100 000-500 000 pairs (Gjershaug et al. 1994). Woodpigeons forage on a wide range of seeds, leaves and some animals during the year (Murton 1965), but during summer and early autumn the diet mainly consists of seeds from crops (Murton 1965, Folk 1984, Cramp 1985, Jimenez et al. 1994). Thus the woodpigeon could be considered a granivorous bird during this part of the year (Jimenez et al. 1994). Due to the facts that it is a gregarious bird and so numerous (Gibbs et al. 2001), it is often regarded as a pest to crops (Murton et al. 1974b), especially for rape *Brassica* (Inglis et al. 1989, Inglis et al. 1997, Gill et al. 1998), peas *Pisum* (legume) and cereal *Poaceae* crops (Jimenez et al. 1994) which are laid, i.e. unharvested crop laid flat by wind (Kenward and Sibly 1977) and precipitation.

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Several researchers have used decoys in their field experiments in bird studies (Root and Yarrow 1967, Murton et al. 1974b, Inglis and Isaacson 1978, Weatherhead and Greenwood 1981, Jeffries and Brunton 2001, Crozier and Gawlik 2003, Green and Leberg 2005, Szymanski and Afton 2005) and some even in woodpigeons research (Inglis and Isaacson 1984, 1987). I used decoys and tactics commonly used by hunters (Murton 1965, Murton et al. 1974b, Batley 2004, Humphreys 2005) to attract woodpigeons on their feeding grounds (Murton et al. 1974b). Flock behaviour experiments were conducted before the woodpigeons were shot and collected for further examination in the laboratory.

Woodpigeon diet is well studied (Murton 1965, Folk 1984, Cramp 1985, Jimenez et al. 1994), but to my knowledge not in Norway. I examined the diet in detail to compare it with woodpigeon diet in other countries. Moreover, I checked for any morphological differences between the sexes, and between juveniles and adults. Then I examined how these differences, in addition to other factors, related to flock behaviour. In addition I investigated which factors that would affect whether a woodpigeon had eaten a specific food item or not before it were shot.

Material and Methods

Study area

Woodpigeons were collected from 21st of August until 30th of September 2005 in Akershus and Østfold County in southeastern Norway (59°26′-59°43′ N and 10°38′-11°16′E). The study area consists of farmland with forest (mostly coniferous forest mixed with miscellaneous deciduous trees) of various sizes in between and around the crop land. In 2005, there was 43599 ha wheat, 39566 ha barley, 36105 ha oat, 4194 ha oilseed rape and turnip rape, 3081 ha rye and 287 ha pea in Akershus (including Oslo) and Østfold counties (pooled), according to Statistics Norway (SSB pers. comm.).

Field work

Decoys made of plastic were used to attract woodpigeons. Either 6, 12 or 20 decoys were placed in a field in an open V-formation facing the wind 3-12 m from the edge of the field (appendix 1). A hiding place for the observers, consisting of a camouflage net (Murton et al. 1974b) and aluminium banksticks, was placed at the edge of the field within shooting range.

Collecting woodpigeons

When a single woodpigeon approached the decoys for landing, the observer tried to shoot it. When a pair of woodpigeons approached the decoys for landing, the observer tried to shoot the first woodpigeon that landed, and then the other one. If a flock (3 or more) approached the decoys for landing, the first woodpigeon was the primary target and other flock members were secondary targets for the observer. If the woodpigeons started to circle over the decoys, but aborted the landing, they were shot if the observer managed to get a clear aim at them.

When a woodpigeon was shoot it was picked up immediately and placed in a plastic bag together with a piece of paper with the actual values for the following variables : shooter, date, distance (m) to the nearest decoy from the hiding place, vegetation type behind the hiding place (straw/rush, scrub, minor trees, or fair-sized trees), hour, time of day (morning/afternoon), type of crop in the field (pea, rape, wheat, rye, barley or oat), cloud cover (clear sky, a few clouds, some clouds, or overcast), precipitation (none, little, some or much), wind speed (none, weak, fair or strong), number of decoys, temperature (C˚), number of woodpigeons in the flock (1, 2 or ≥3), landing number in the flock (first woodpigeon to land in the flock, second or later), and whether the shot woodpigeon had landed or aborted landing. After the observation session was finished, the woodpigeons were put in a freezer and stored at -22℃. A total of 121 woodpigeons were shot.

Laboratory work

At the laboratory I first checked whether the white neck band was present or not (this is an index on development since all the adults and the juveniles that have moulted have it (Cramp 1985)). Then the woodpigeon was weighed on a digital scale with an accuracy of 0.01g. The tail length were measured with an accuracy of 1mm with a ruler according to Svensson (1992). The wing length were measured with an accuracy of 1mm with a ruler and taken from the body of the woodpigeon to the tip of longest primary feather in stretched state. Bill length were measured with an accuracy of 0.1 mm with a digital slide caliper and measured from the tip of the bill to the corner of the mouth. Bill height, tarsus length (bent), and length of the claw on the middle toe were measured with an accuracy of 0.1 mm with a digital slide caliper according to Svensson (1992). Length of the middle toe was measured with an accuracy of 0.1 mm with a digital slide caliper from the first segment under the toe and to the beginning of the claw. The woodpigeon were dissected by removing the crop with its content for further study (see below). The sex was determined by checking whether the gonads consisted of eggs or testicles.

Separating adult from juveniles

Juveniles and adult woodpigeons were separated following Cramp (1985). Following Cramp (1985) all males with tail length ≥161mm and all females with tail length ≥157mm were classified as adults, and all males with tail length ≤155mm and females with tail length ≤147mm were classified juveniles. All woodpigeons without white neck band were classified as juveniles. The other morphologic character that differed significantly between adults and juveniles, according to Cramp (1985) was wing length. Unfortunately, I measured wing length differently than the studies referred to in Cramp (1985). Therefore, before my study could be compared with those in Cramp (1985), the average for the sexes was calculated. On average, the values I recorded were 79 mm longer for the males and 74 mm longer for the females, than those referred to in Cramp (1985). Therefore, I subtracted 79 mm from the measured wing length of each male and 74 mm from the measured wing length of each female. Then, according to Cramp (1985), males with wing length ≥252 mm, and females with wing length ≥252 mm, were classified as adults. Correspondingly, males with wing length ≤240 mm and females with wing length ≤239 mm were classified as juveniles. Still, 15 woodpigeons remained unclassified. To classify these, the average tail length, wing length, tarsus length, bill length, bill high, length of middle toe and middle toe claw, body weight, were calculated for males and females separately. Then, if a woodpigeon had no more than four of these eight variables above the average it was classified as a juvenile. If it had at least five of the eight variables above the average it was classified as an adult. Only one male and one female were classified as adults from this method, and they both had seven of the eight morphological variables above the average.

Analysis of crop

Of the 121 woodpigeons shot, 82 had at least one item in the crop. (Here "crop" means a thin-walled bag used for the storage of food prior to digestion found in birds, but in other parts of the paper it also means: a plant that is grown in large quantities to be harvested as food.) Of these, ten were not examined further than to see if they had eaten or not, due to for instance the crop being damaged by the shot. The remaining 72 woodpigeons were examined in detail, their crop content was analyzed by opening the crop and removing its content into a Petri dish (Jimenez et al. 1994). Several woodpigeons had a fat layer inside the crop that had parted from the crop and been mixed together with the crop content, which was removed with a pincer. The Petri dishes were individually marked and then stored in a fairly warm and dry room for a week, so that surplus water would evaporate and the percent dry substance content would be approximately the same in every sample. After this drying period the crop samples were sorted to species or as close as possible. The sorted samples were weighed separately on a digital scale with an accuracy of 0.0001 g. The woodpigeon's net weight was calculated by subtracting the total weight of all dried samples in the crop from the recorded body weight.

To compare availability with eaten or not, the percent of number of woodpigeons that had eaten different food items were divided with the percent average share of the different crops was calculated. It was not possible to make a complete accurate calculation of the total area when it came to peas, since the farmers report it in tree different posts (according to range of application) in the questionnaire form sent to the government and all tree posts are pooled with different types of crops. Therefore, it was made an assumption on how much of the three posts that consisted of peas and then got an approximately figure.

Statistic

Statistical analysis was performed with JMP version 4.0 (SAS 2000), figures were constructed with Office Excel (Microsoft 2003) and JMP version 4.0 (SAS 2000), tables were constructed with Office Word (Microsoft 2003), and appendix sketches were constructed with Office Paint (Microsoft 2003). Oneway ANOVA was used to test for differences between two samples. I used two-way ANOVA to test difference between juvenile and adults, and males and females, on the morphologic characteristics. For one- and two-way ANOVA, data were tested for normality, and transformed if necessary.

To examine flock behaviour I used logistic regression analyzes by backward elimination of non-significant effects to test if nominal response variables (sex, age, landing number in the flock, and flock composition) were significantly affected by different independent variables (flock composition, number of decoys, temperature, cloud cover, precipitation, vegetation type behind the hiding place, wind speed, time of the day, distance to the nearest decoy from the hiding place, landing number in the flock, date, type of crop in the actual field, whether the woodpigeon had eaten or not, sex, age and weight).

I also used logistic regression analyzes by backward elimination of non-significant effects to examine which independent variables (length of claw on the middle toe, tail length, bill height, tarsus length, age, vegetation type behind the hiding place, distance to the nearest decoy from the hiding place, time of day, landing number inn the flock, bill length, temperature, sex, wind speed, middle toe length, precipitation, date, number of woodpigeons in the flock, type of crop and net weight (type of crop were not present in all tests)) that had a significant effect on whether the woodpigeon had eaten a specific food item or not before it was shot.

At some type of crops very few woodpigeons were shot. Including these woodpigeons in test where crop type was one of the independent variables often resulted in unstable test results. In these cases, the woodpigeons shot at these types of crop were excluded, and the test repeated.

Results

Morphology

A total of 121 woodpigeons were shot during the study. Of these, 29 were adult males, 38 juvenile males, 21 adult females, and 33 juvenile females. Thus, there were 50 adults and 71 juveniles, and the sex ratio was 67 males and 54 females.

Tarsus length

Tarsus length of the shot woodpigeons was significantly larger for males than for females, and significantly larger for adults than for juveniles (Table 1; two-way ANOVA, $F_{2, 117} = 8.70$, p=0.0003, F = 11.14, p = 0.001 for sex, F = 5.52, p = 0.021 for age).

Table 1. Tarsus length (mm) of the woodpigeons shot, shown as mean ± SE, with range and sample size in parenthesis.

	Males	Females	All
Juveniles	30.7±0.2 (27.3–32.8)(38)	30.1±0.2 (26.9–31.8)(33)	30.4±0.1 (29.9-32.8)(71)
Adults	31.2±0.2 (28.9-32.8)(29)	30.5±0.2 (29-33.3)(21)	30.9±0.1 (28.9-33.3)(50)
All	30.9±0.1 (27.3-32.8)(67)	30.2±0,2 (26.9-33.3)(54)	30.6±0.1 (26.9-33.3)(121)

Tail length

Tail length of the shot woodpigeons was significantly larger for males than for females, and significantly larger for adults than for juveniles (Table 2; two-way ANOVA, $F_{2, 118} = 74.00$, p<0.0001, F = 54.87, p <0.0001 for sex, F = 86.71, p = <0.0001 for age).

Table 2. Tail length (mm) of the woodpigeons shot, shown as mean ± SE, with range and sample size in parenthesis.

	Males	Females	All
Juveniles	152.1±0.8 (140–160)(38)	145.5±1.2 (128–156)(33)	149±0.8 (128-160)(71)
Adults	161.7±0.9 (156-174)(29)	153.4±0.9 (148-165)(21)	158.3±0.8 (148-174)(50)
All	156.2±0.8 (140-174)(67)	148.7±1.0 (128-165)(54)	152.9±0.7 (128-174)(121)

Wing length

Wing length of the shot woodpigeons was significantly larger for males than for females, and significantly larger for adults than for juveniles (Table 3; two-way ANOVA, $F_{2, 118} = 58.44$, $p<0.0001$, $F = 17.31$, $p =<0.0001$ for sex, $F = 95.73$, $p = <0.0001$ for age)

Table 3. Wing length (mm) of the woodpigeons shot, shown as mean ± SE, with range and sample size in parenthesis.

	Males	Females	All
Juveniles	322.2±1.0 (307–333)(38)	316.2±1.5 (293–330)(33)	319.4±0.9 (293-333)(71)
Adults	333.6±1.1 (322-346)(29)	329.6±1.2 (313-342)(21)	331.9±0.9 (313-346)(50)
All	327.1±1.0 (307-346)(67)	321.4±1.4 (293-342)(54)	324.6±0.9 (293-346)(121)

Bill length

Bill length was significantly larger for adults than for juveniles, but did not differ significantly between males and females (Table 4; two-way ANOVA, $F_{2, 117} = 4.27$, $p = 0.016$, $F = 6.17$, $p = 0.014$ for age, $F = 2.09$, $p = 0.15$ for sex)

Table 4. Bill length (mm) of the woodpigeons shot, shown as mean ± SE, with range and sample size in parenthesis.

Juveniles	28.0±0.1 (26-31.3)(70)
Adults	28.5±0.1 (23.1-30.7)(50)
All	28.2±0.1 (26-31.3)(120)

Bill height

Bill height of the shot woodpigeons was significantly larger for males than for females, and significantly larger for adults than for juveniles (Table 5; two-way ANOVA, $F_{2, 117} = 8.61$, $p = 0.0003$, $F = 6.78$, $p = 0.010$ for sex, $F = 9.82$, $p = 0.0022$ for age)

Table 5. Bill height (mm) of the woodpigeons shot, shown as mean ± SE, with range and sample size in parenthesis.

	Males	Females	All
Juveniles	7.6±0.1 (6.7–8.5)(38)	7.4±0.0 (6.2–8.2)(32)	7.5±0.1 (6.2-8.5)(70)
Adults	7.9±0.1 (7.2-8.9)(29)	7.6±0.1 (6.7-8.7)(21)	7.8±0.1 (6.7-8.9)(50)
All	7.7±0.1 (6.7-8.9)(67)	7.5±0.1 (6.2-8.7)(53)	7.6±0.0 (6.2-8.9)(120)

Middle toe length

Middle toe length of the shot woodpigeons was significantly larger for males than for females, and significantly larger for adults than for juveniles (Table 6; two-way ANOVA, $F_{2, 118} = 8.98$, $p = 0.0002$, $F = 9.77$, $p = 0.0022$ for sex, $F = 7.41$, $p = 0.0075$ for age)

Table 6. Middle toe length (mm) of the woodpigeons shot, shown as mean ± SE, with range and sample size in parenthesis.

	Males	Females	All
Juveniles	28.6±0.2 (26.4–30.7)(38)	28.0±0.2 (25.5–29.4)(33)	28.3±0.1 (25.5-30.7)(71)
Adults	30.0±0.2 (27.2-31.2)(29)	28.5±0.2 (26.5-30.1)(21)	28.7±0.1 (26.5-31.2)(50)
All	28.7±0.1 (26.4-31.2)(67)	28.2±0.1 (25.5-30.1)(54)	28.5±0.1 (25.5-31.2)(121)

Claw length

Length of claw on the middle toe was significantly larger for adults than for juveniles, but did not differ significantly between males and females (Table 7; two-way ANOVA, $F_{2, 118} = 7.57$, $p = 0.0008$, $F = 12.68$, $p = 0.0005$ for age, $F = 1.99$, $p = 0.16$ for sex)

Table 7. Length of claw on the middle toe (mm) of the woodpigeons shot, shown as mean ± SE, with range and sample size in parenthesis.

Juveniles	10.0±0.1 (7.8-18.8)(71)
Adults	10.6±0.1 (8.6-12)(50)
All	10.3±0.1 (7.8-12.8)(121)

Net weight

Net weight (raised to third power) of the shot woodpigeons were significantly larger for males than for females, and significantly larger for adults than for juveniles (Table 8; two-way ANOVA, $F_{2, 117} = 8.61$, $p = 0.0003$, $F = 6.78$, $p = 0.010$ for sex, $F = 9.82$, $p = 0.0022$ for age)

Table 8. Net weight (g) of the woodpigeons shot, shown as mean ± SE, with range and sample size in parenthesis.

	Males	Females	All
Juveniles	469.5±9.1 (355.1–554.0)(31)	450.0±7.7 (335.6–517.2)(33)	459.4±6.0 (335.6-554.0)(64)
Adults	504.8±5.2 (462.3-559.8)(28)	486.4±5.3 (446.9-559.8)(18)	497.6±4.0 (446.9-559.8)(46)
All	486.3±5.8 (355.1-559.8)(59)	462.9±5.8 (335.6-539.8)(51)	475.4±4.2 (335.6-559.8)(110)

White neck band

Of the 71 juvenile woodpigeons shot, 60 had the white neck band and 11 were without. The probability of with neck band increased with weight (fig. 1, Logistic regression: $X^2 = 29.51$, df = 1, p< 0.0001, intercept = -19.93 ± 5.69, slope (weight) = 0.049 ± 0.013).

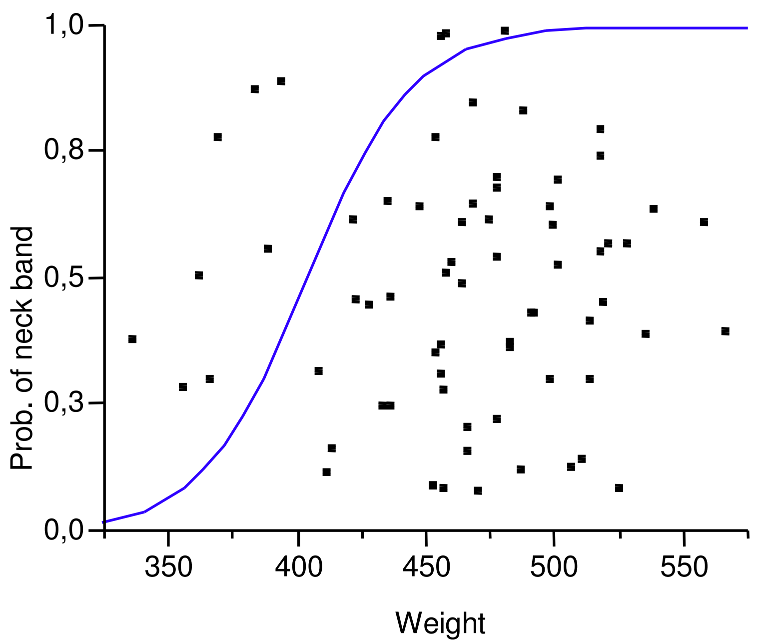

Fig 1. The probability of the juveniles having a white neck band increased with increasing weight.

Flock behaviour

In a logistic regression model with flock composition as a response and distance to the nearest decoy from the hiding place, sex, weight, vegetation type behind the hiding place, number of decoys, date, type of crop in the actual field, whether the woodpigeon had eaten or not, wind speed, age, temperature and time of the day as independent variables (removed in the given order), temperature and time of the day had a significant effect (table 9). The probability of being in a flock increased with increasing temperature and were highest in the afternoon. Thus, there was no significant relationship between flock composition and sex and age of the woodpigeon (fig. 2).

Table 9. Logistic regression model of significant effects on flock composition. Whole model N = 121, x^2 = 15.58, df = 2, P = 0.0004.

Variable	df	x^2	P
Temperature	1	4.85	0.0277
Time of the day	1	11.60	0.0007

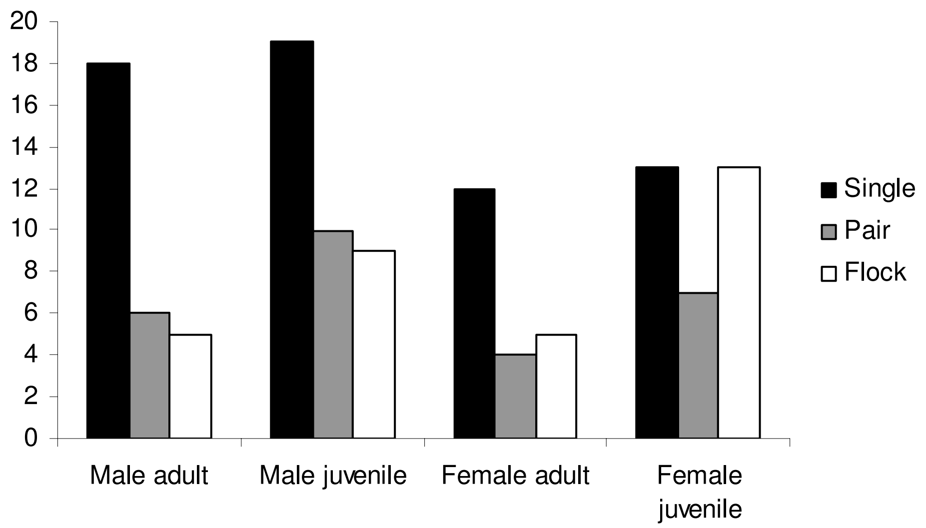

Fig 2. Flock composition, age and sex distribution of the shot woodpigeons.

In a logistic regression model with sex as response, and flock composition, number of decoys, temperature, cloud cover, precipitation, vegetation type behind the hiding place, wind speed, time of the day, distance to the nearest decoy from the hiding place, landing number in the flock, date, type of crop in the actual field and whether the woodpigeon had eaten or not as independent variables, no variable had any significant effect.

In a logistic regression model with age as response, and flock composition, number of decoys, temperature, cloud cover, precipitation, vegetation type behind the hiding place, wind speed, time of the day, distance to the nearest decoy from the hiding place, landing number in the flock, date, type of crop in the actual field and whether the woodpigeon had eaten or not as independent variables, no variable had any significant effect.

In a logistic regression model with landing number in the flock as response, and sex, age, flock composition, weight, temperature, vegetation type behind the hiding place, wind speed, time of the day, distance to the nearest decoy from the hiding place, date, type of crop in the actual field and whether the woodpigeon had eaten or not as independent variables, no variable had any significant effect.

Diet

Of the woodpigeons in flock, 50% had eaten, compared to 82% of woodpigeons in pairs and 71% of single woodpigeons (fig. 3).

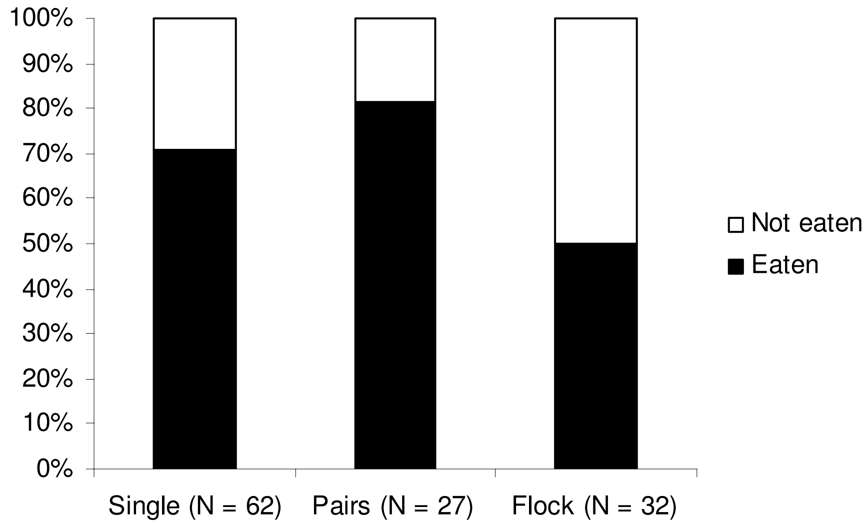

Fig. 3. Percent of the woodpigeons that had eaten (had food in their crop) in relation to whether they were flying alone, in pair or in a flock when shot. Likelihood ratio test, $N = 121$, $X^2 = 7.18$, $df = 2$, $P = 0.028$.

Oilseed rape and turnip rape (pooled)

Of the 72 woodpigeons which had the crop content examined in detail, 12 had eaten rape (fig. 4). For these 12 the mean dry weight of rape in the crop was 3.1 ± 0.7 g, with range 0.004-7.8 g. The total weight of rape consumed by the woodpigeons in this study was 37.0 g (7.7% of all eaten material). In a logistic regression model with whether the woodpigeon had eaten oilseed rape and turnip rape or not as response, and precipitation, landing number in the flock, date, claw on the middle toe length, temperature, time of day, wind speed, number of woodpigeons in the flock, tarsus length, bill height, sex, tail length, net weight, bill length, vegetation type behind the hiding place, age, middle toe length, distance to the nearest decoy from the hiding place as independent variables (removed in the given order), age, middle toe length, distance to the nearest decoy from the hiding place had a significant effect (table 10). The probability of having eaten rape was higher for juveniles than adults, increased with increasing middle toe length, and increased with increasing distance to the nearest decoy from the hiding place.

Of the 72 woodpigeons that had their crop examined in detail, wheat exhibited the highest percent eaten and oat the lowest (fig. 4).

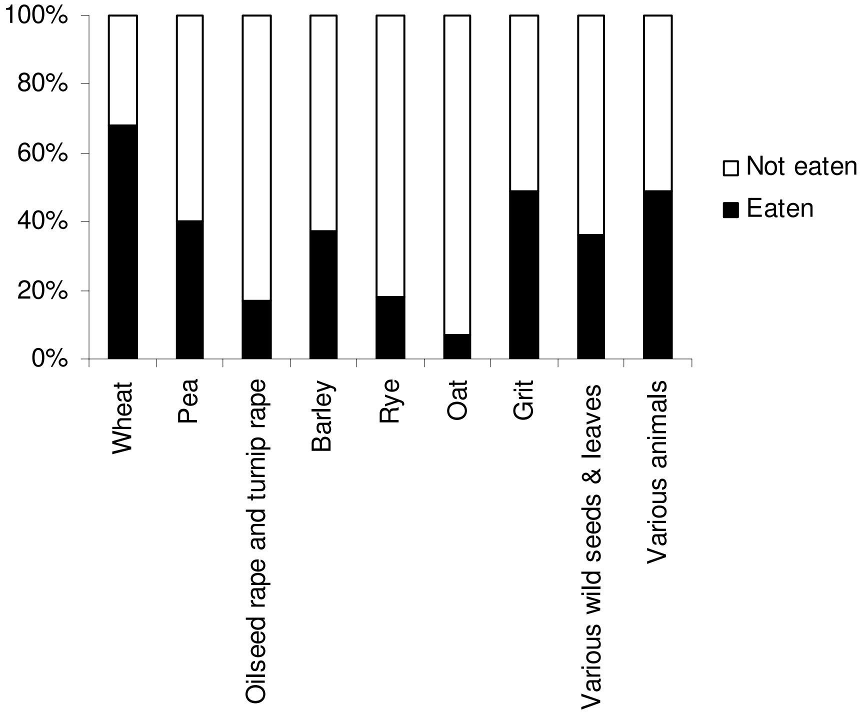

Fig 4. Percentage of woodpigeons examined in detail that had a food type present in the crop (N = 72).

Table 10. Logistic regression model of significant effects on whether the woodpigeon had eaten oilseed rape and turnip rape or not. Whole model N = 111, x^2 = 20.09, df = 3, P = 0.0002.

Variable	df	x^2	P
Age	1	5.15	0.0233
Middle toe length	1	6.25	0.0124
Distance to the nearest decoy from the hiding place	1	17.10	<0.0001

Barley

Of the 72 woodpigeons which had the crop content examined in detail, 27 had eaten barley (fig. 4). For these 27, the mean dry weight of eaten barley was 2.8 ± 0.6 g, with range 0.05-11.2 g. The total dry weight of barley consumed by the woodpigeons in this study was 76.8 g (16.0% of all eaten material). In a logistic regression model with whether the woodpigeon had eaten barley or not as a response, and number of woodpigeons in the flock, landing number in the flock, vegetation type behind the hiding place, bill length, distance to the nearest decoy from the hiding place, temperature, claw on the middle toe length, date, precipitation, tail length, wind speed, middle toe length, sex, age, net weight, bill height, time of day, and tarsus length as independent variable (removed in the given order), sex, age, net weight, bill height, time of day, and tarsus length had a significant effect (table 11). The probability of having eaten barley was higher for males and juveniles than females and adults, increased with increasing net weight, increased with increasing bill height, were higher in the morning than in the evening and decreased with increasing tarsus length.

Table 11. Logistic regression model of significant effects on whether the woodpigeon had eaten barley or not. Whole model N = 109, x^2 = 37.45, df = 6, P = 0.0001.

Variable	df	x^2	P
Sex	1	4.45	0.0348
Age	1	4.95	0.0260
Net weight	1	8.09	0.0045
Bill height	1	8.50	0.0036
Time of day	1	13.24	0.0003
Tarsus length	1	15.17	0.0001

Rye

Of the 72 woodpigeons which had the crop content examined in detail, 13 had eaten rye (fig. 4). For these 13, the mean dry weight of eaten rye was 2.5 ± 1.0 g, with range 0.03-10.0 g. The total dry weight of barley consumed by the woodpigeons in this study was 31.9 g (6.6% of all eaten material). In a logistic regression model with whether the woodpigeon had eaten rye or not as response, and age, precipitation, middle toe length, wind speed, tail length, distance to the nearest decoy from the hiding place, landing number in the flock, bill length, tarsus length, time of day, sex, temperature, net weight, length of claw on the middle toe, number of woodpigeons in the flock, date, vegetation type behind the hiding place and bill height as independent variables (removed in the given order), only bill height had a significant effect (x^2 = 4.06, df = 1, P = 0.044). The probability of having eaten rye increased with increasing bill height.

Oat

Of the 72 woodpigeons which had the crop content examined in detail, 5 had eaten oat (fig. 4). For these 5, the mean dry weight of eaten oat was 2.5 ± 2.3 g, with range 0.03-11.8 g. The total weight of oat consumed by the woodpigeons in this study was 12.4 g (2.6% of all eaten material). In a logistic regression model with whether the woodpigeon had eaten oat or not as response, and date, age, precipitation, bill height, bill length, landing number in the flock, tarsus length, length of claw on the middle toe, net weight, sex, distance to the nearest decoy from the hiding place, number of woodpigeons in the flock, time of day, vegetation type behind the hiding place, temperature, middle toe length, and tail length as independent variables (removed in the given order), no variable had any significant effect.

Wheat

Of the 72 woodpigeons which had the crop content examined in detail, 49 had eaten wheat (fig. 4). For these 49, the mean dry weight of eaten wheat was 3.3 ± 0.8 g, with range 0.006-22.9 g. The total weight of wheat consumed by the woodpigeons in this study was 160.7 g (33.4% of all eaten material). In a logistic regression model with whether the woodpigeon had eaten wheat or not as response, and time of day, date, length of claw on the middle toe, age, temperature, tarsus length, middle toe length, bill height, bill length, sex, landing number in the flock, tail length, vegetation type behind the hiding place, distance to the nearest decoy from the hiding place, rain presence, number of woodpigeons in the flock, wind speed, net weight, and type of crop as independent variable (removed in the given order), vegetation type behind the hiding place, distance to the nearest decoy from the hiding place, precipitation, number of woodpigeons in the flock, wind speed, net weight and type of crop had a significant effect (table 12). The probability of having eaten wheat decreased with increasing height of the vegetation type behind the hiding place, decreased with increasing distance to the nearest decoy from the hiding place, were highest with little precipitation and lowest with some precipitation, were highest with woodpigeons in pairs and lowest with woodpigeons in flocks, highest with fair wind and lowest with weak or strong wind, increased with increasing net weight, and were highest in wheat fields and lowest in barley fields.

Table 12. Logistic regression model of significant effects on whether the woodpigeon had eaten wheat or not. Whole model N = 100, x^2 = 41.41, df = 13, P = 0.0001.

Variable	Df	x^2	P
Vegetation type behind the hiding place	2	7.75	0.0208
Distance to the nearest decoy from the hiding place	1	5.68	0.0172
Precipitation	2	10.49	0.0053
Number of woodpigeons in the flock	2	10.99	0.0041
Wind speed	3	14.12	0.0027
Net weight	1	10.42.	0.0012
Type of crop	2	13.74	0.0010

Pea

Of the 72 woodpigeons which had the crop content examined in detail, 29 had eaten peas (fig. 4). For these 29, the mean dry weight of eaten peas was 4.7 ± 1.1 g, with range 0.23-23.4 g. The total dry weight of peas consumed by the woodpigeons in this study was 135.7 g (28.2% of all eaten material). In a logistic regression model with whether the woodpigeon had eaten pea or not as response, and bill length, number of woodpigeons in the flock, landing number in the flock, tail length, time of day, distance to the nearest decoy from the hiding place, sex, middle toe length, length of claw on the middle toe, temperature, precipitation, tarsus length, bill height, age, wind speed, vegetation type behind the hiding place, date and net weight as independent variables (removed in the given order), wind speed, vegetation type behind the hiding place, date and net weight had a significant effect (table 13). The probability of having eaten peas were highest with strong wind and lowest with fair wind, were highest when vegetation type behind the hiding place where minor trees, decreased as the days went by in the study period, and increased with increasing net weight.

Table 13. Logistic regression model of significant effects on whether the woodpigeon had eaten peas or not. Whole model N = 109, x^2 = 29.93, df = 7, P = < 0.0001.

Variable	df	x^2	P
Wind speed	3	7.99	0.0461
Vegetation type behind the hiding place	2	7.70	0.0212
Date	1	9.96	0.0016
Net weight	1	11.41	0.0007

Grit

Of the 72 woodpigeons which had the crop content examined in detail, 35 had eaten grit (fig. 4). For these 35, the mean dry weight of eaten grit was 0.6 ± 0.2 g, with range 0.01-5.6 g. The total dry weight of grit consumed by the woodpigeons in this study was 20.0 g (4.2% of all eaten material). A few woodpigeons had also some sand in their crop, perhaps taken in with the food or eaten as grit. Two woodpigeons had also eaten tubeworms (Polychaeta), most likely fossils, probably to obtain mineral resources. Both the sand and the tubeworms were pooled with the grit. In a logistic regression model with whether the woodpigeon had eaten grit or not as response, and number of woodpigeons in the flock, length of claw on the middle toe, time of day, age, sex, tail length, distance to the nearest decoy from the hiding place, vegetation type behind the hiding place, bill length, middle toe length, precipitation, wind speed, temperature, landing number in the flock, date, tarsus length, bill height and net weight as independent variables (removed in the given order), only net weight had a significant effect (X^2 = 7.55, df = 1, P = 0.0060). The probability of having eaten grit increased with increasing net weight.

Various wild seeds and leaves (pooled)

Of the 72 woodpigeons which had the crop content examined in detail, 26 had eaten native vegetable matter (mostly seeds) (fig. 4). For these 26, the mean dry weight of eaten native vegetable matter was 0.1 ± 0.1 g, with range 0.001-2.5 g (of one type of native vegetable matter). The total dry weight of native vegetable matter consumed by the woodpigeons in this study was 3.6 g (0.8% of all eaten material). Plant species found were (state, number of crops, and mean weight in parenthesis); clover family (Trifolium) (leaf, N = 14, mean = 0.04 ± 0.01 g), pink family (Caryophyllaceae) (seed, N = 10, mean = 0.02 ± 0.007 g), mustard family

(Brassicaceae) (seed, N = 4, mean = 0.07 ± 0.07 g), prunus genus (*Prunus*) (seed, N = 1, weight = 0.04 g), sedge family (Cyperaceae) (seed, N = 1, weight = 0.002 g), sunflower (*Helianthus annuus*) (seed, N = 1, weight = 2.5 g), rose family (Rosaceae) (leaf, N = 1, weight = 0.02 g), unknown seeds (N = 2, mean = 0.002 ± 0.0008 g), unknown leaf (N = 1, weight = 0.003 g), unknown twig with traces of an seed capsule (N = 1, weight = 0.004 g) and unknown capsule (vegetable or animal) (N = 2, mean = 0.02 ± 0.02 g). Over half of the woodpigeons had not eaten any type of wild seeds and leaves (table 14). In a logistic regression model with whether the woodpigeon had eaten various wild seeds and leaves or not as response, and tarsus length, date, landing number in the flock, time of day, sex, tail length, temperature, length of middle toe, age, net weight, claw on the middle toe length, bill length, bill height, vegetation type behind the hiding place, wind speed, type of crop, number of woodpigeons in the flock, distance to the nearest decoy from the hiding place and precipitation as independent variables (removed in the given order), length of claw on the middle toe, bill length, bill height, vegetation type behind the hiding place, wind speed, type of crop, number of woodpigeons in the flock, distance to the nearest decoy from the hiding place, and precipitation had a significant effect (table 15). The probability of having eaten wild seeds and leaves increased with increasing length of claw on the middle toe, decreased with increasing bill length, increased with increasing bill height, were highest with lowest vegetation type behind the hiding place, increased with increasing wind speed, were highest in wheat fields and lowest in barley fields, were highest in pairs and lowest in flocks, decreased with increasing distance to the nearest decoy from the hiding place, and were lowest with some precipitation.

Table 14. Number of different wild seeds and leaves (of 12 possible) present in the woodpigeons crops.

Number of types of various wild plants in a woodpigeon	Number of woodpigeons	% of woodpigeons
0	46	63.9
1	17	23.6
2	6	8.3
3	3	4.2
Total	72	100

Table 15. Logistic regression model of significant effects on whether the woodpigeon had eaten various wild seeds and leaves or not. Whole model N = 100, x^2 = 47.86, df = 15, P = <0.0001.

Variable	df	X^2	P
Length of claw on the middle toe	1	4.94	0.0262
Bill length	1	5.13	0.0235
Bill height	1	5.19	0.0227
Vegetation type behind the hiding place	2	8.09	0.0175
Wind speed	3	10.87	0.0124
Type of crop	2	9.79	0.0075
Number of woodpigeons in the flock	2	9.87	0.0072
Distance to the nearest decoy from the hiding place	1	7.60	0.0058
Precipitation	2	10.36	0.0056

Various animals (pooled)

Of the 72 woodpigeons which had the crop content examined in detail, 35 had eaten animal nourishment (fig. 4). For these 35, the mean dry weight eaten of animal nourishment was 0.1 ± 0.03 g, with range 0.001-0.66 g. The total dry weight of animal nourishment consumed by the woodpigeons in this study was 3.0 g (0.6% of all eaten material). Animal species found were (number of crops and mean weight in parenthesis); snail (Gastropoda) (N = 30, mean = 0.09 ± 0.03 g), caterpillar (Lepidoptera) (or other species of larva) (N = 4, mean = 0.05 ± 0.01 g), earthworm cocoon (Lumbricina) (N = 1, weight = 0.0058 g) and weevil (Curculionoidea) (N = 1, weight = 0.0011 g). Almost half of all the woodpigeons in my study had one or two types of animal nourishment remnants in their crop (table 16). In a logistic regression model with whether the woodpigeon had eaten various animals or not as response, and temperature, length of claw on the middle toe, bill length, landing number inn the flock, tail length, age, tarsus length, sex, middle toe length, bill height, number of woodpigeons in the flock, wind speed, type of crop, distance to the nearest decoy from the hiding place, vegetation type behind the hiding place, time of day, precipitation, net weight, and date as independent variables (removed in the given order), wind speed, type of crop, distance to the nearest decoy from the hiding place, vegetation type behind the hiding place, time of day, precipitation, net weight and date had a significant effect (table 17). The probability of having eaten various animals were highest with strong wind and were lowest with fair wind, were highest on wheat fields and lowest on barley fields, increased with increasing distance to the nearest decoy from the hiding place, were highest with lowest vegetation type behind the hiding place, higher in the morning, were highest in little precipitation and lowest in some precipitation, increased with increasing net weight, and decreased as the days went by.

Table 16. Number of different animals (of 5 possible) present in the woodpigeons crops. Empty crops excluded.

Number of types of various animals in a woodpigeon	Number of woodpigeons	% woodpigeons
0	38	52.8
1	32	44.4
2	2	2.8
Total	72	100

Table 17. Logistic regression model of significant effects on whether the woodpigeon had eaten various animals or not. Whole model N = 100, x^2 = 40.50, df = 13, P = <0.0001.

Variable	df	X^2	P
Wind speed	3	8.66	0.0342
Type of crop	2	9.52	0.0086
Distance to the nearest decoy from the hiding place	1	8.24	0.0041
Vegetation type behind the hiding place	2	12.09	0.0024
Time of day	1	9.36	0.0022
Precipitation	2	14.34	0.0008
Net weight	1	11.38	0.0007
Date	1	14.44	0.0001

All crops (pooled)

All the 72 woodpigeons that had the crop content examined in detail had eaten at least one type of crop (table 18). For these 72, the mean dry weight of eaten crop was 6.1 ± 0.8 g, with range 0.004-33.5 g. The total weight of crops consumed by the woodpigeons in this study was 436.9 g (94.4% of all eaten material). In a logistic regression model with whether the woodpigeon had eaten any crop or not as response, length of and claw on the middle toe, tail length, bill height, tarsus length, age, vegetation type behind the hiding place, distance to the nearest decoy from the hiding place, time of day, landing number in the flock, bill length, temperature, sex, wind speed, middle toe length, precipitation, date, number of woodpigeons in the flock, type of crop and net weight as independent variables (removed in the given order), number of woodpigeons in the flock, type of crop, and net weight had a significant effect (table 19). The probability of having eaten any crop were highest in pairs and lowest in flocks, were highest on wheat fields and lowest on barley fields, and increased with increasing net weight. For the woodpigeons that had eaten and were shot in pea fields mean dry weight of food eaten was 7.08 ± 1.15 g, with range 0.042-28.38 g, whereas the total mean dry weight of food eaten for all the woodpigeons shot in pea fields was 4.58 ± 0.85 g, with range 0.0-28.38 g. For the woodpigeons that had eaten and were shot in wheat fields mean dry weight of food eaten was 6.03 ± 1.7 g, with range 0.23-24.32 g, whereas the total mean dry weight of food eaten for all the woodpigeons shot in wheat fields was 4.52 ± 1.4 g, with range 0.0-24.32 g. The woodpigeons that had eaten and were shot in barley fields had in mean dry weight eaten 3.04 ± 1.73 g, with range 0.023-8.31 g, whereas the total mean dry weight of all the woodpigeons shot in barley fields were 1.09 ± 0.7 g, with range 0.0-8.31 g.

Table 18. Number of different crops (of 6 possible) present in the woodpigeon's crop. Woodpigeons with empty crops excluded.

Number of types of crops in a woodpigeon	Number of woodpigeon	% woodpigeon
0	0	0
1	33	45.8
2	23	31.9
3	9	12.5
4	6	8.3
5	1	1.4
Total	72	99.9

Table 19. Logistic regression model of significant effects on whether the woodpigeon had eaten any crop or not. Whole model N = 101, x^2 = 30.16, df = 5, P = <0.0001.

Variable	df	x^2	P
Number of woodpigeons in the flock	2	8.77	0.0125
Type of crop	2	12.81	0.0017
Net weight	1	15.71	0.0001

All food items (pooled)

For the 72 woodpigeons examined in detail in this study (see above in method), the mean dry weight of eaten material was 6.7 ± 0.9 g, with range 0.004-33.5 g. The total dry weight of material consumed by the woodpigeons in this study was 481.1 g, and included twelve different wild vegetable matter (mostly seeds), five different animal types, six different crops, and grit (tables 14, 16, 18 and 20). In a logistic regression model with whether the woodpigeon had eaten any food item or not as response, and length of claw on the middle toe, tail length, bill height, tarsus length, age, vegetation type behind the hiding place, distance to the nearest decoy from the hiding place, time of day, landing number in the flock, bill length, temperature, sex, wind speed, middle toe length, precipitation, date, number of woodpigeons in the flock, type of crop, and net weight as independent variables (removed in the given order), number of woodpigeons in the flock, type of crop and net weight had a significant effect (table 21). The probability of having eaten any crop were highest in pairs and lowest in flocks, were highest on wheat fields and lowest on barley fields, and increased with increasing net weight.

Table 20. Number of different types of items (of 24 possible) present in the woodpigeons crop. Woodpigeons with empty crop excluded.

Number of types of items in a woodpigeons	Number of woodpigeons	% woodpigeons
1	15	20.8
2	13	18.1
3	9	12.5
4	16	22.2
5	9	12.5
6	6	8.3
7	2	2.8
8	1	1.4
9	1	1.4
Total	72	100

Table 21. Logistic regression model of significant effects on whether the woodpigeon had eaten or not. Whole model N = 101, x^2 = 30.16, df = 5, P = <0.0001.

Variable	df	x^2	P
Number of woodpigeons in the flock	2	8.77	0.0125
Type of crop	2	12.81	0.0017
Net weight	1	15.71	0.0001

For the 72 woodpigeons which had the crop content examined in detail the dry mean weight of the content were 6.7 ± 0.9 g. In comparison the difference between the woodpigeons that had eaten (485.7 ± 4.1 g) and those who had not eaten (456.6 ± 8.6 g, N = 39) were 29.1 g, which was highly significant (Oneway ANOVA: F= 11.80, df= 1, P = 0.0008, N=110).

Wheat, barley and oat cover roughly an equal share of the farmland, but barley and oat were eaten in much smaller degree than wheat in proportion to the availability (fig. 5).

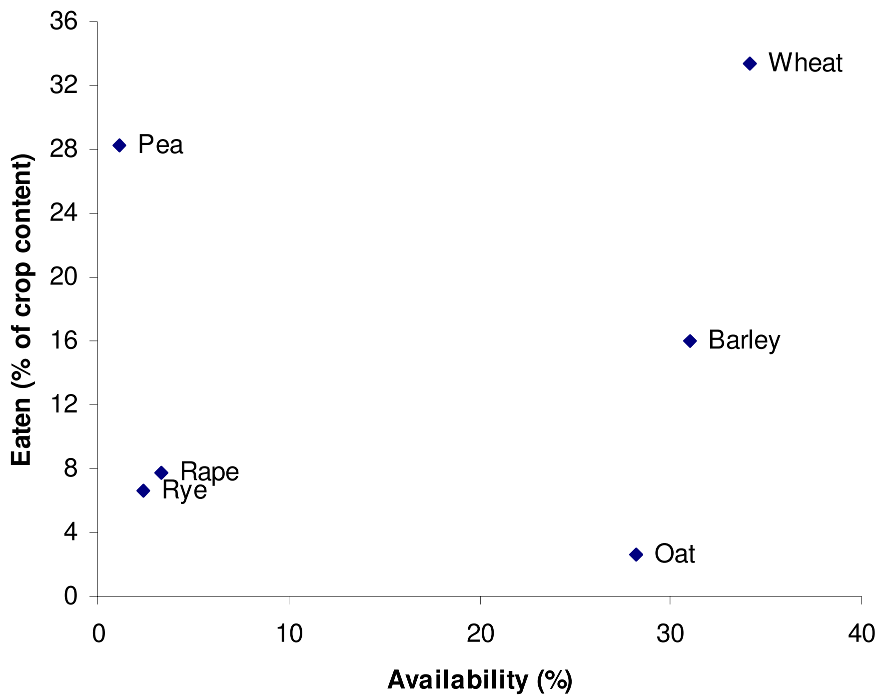

Fig 5. Eaten different crops versus the availability of the crop.

Wheat was the most eaten crop both in percent of woodpigeons that had eaten, and in percent of total dry weight of all crop content. However, peas were the most eaten in percent in proportion to the availability of the crop (table 22).

Table 22. Percent eaten of different crops, the availability of the crop (average between Østfold and Akershus) and preference index (percent eaten divided with percent available).

Type of crop	Percent of woodpigeons with crop type	Percent of woodpigeons total crop content	Availability of crop (ha)	(%)	Preference index
Wheat	68.1	33.4	43599	34.1	1
Pea	40.3	28.2	278	1.1	25.6
Rape*	16.7	7.7	4194	3.3	2.3
Barley	37.5	16.0	39566	31.0	0.5
Rye	18.1	6.6	3081	2.4	2.8
Oat	6.9	2.6	36105	28.2	0.1

* Oilseed rape and turnip rape.

Discussion

Morphological characters

Tarsus length

I measured the mean tarsus length to be 30.9 mm for males and 30.2 mm for females. According to Cramp (1985) the mean tarsus length is 32.8 mm for males and 32.7 mm for females. There are several possibilities for these differences. First, my sample was nearly twice as large as the one referred to in Cramp (1985). Second, my sample is from a relatively short period of time, shortly after the juveniles from the second and last brood of the year had fledged cf. (Murton 1965, Haftorn 1971), and over half of my sample consisted of juveniles (N = 71). The studies referred to in Cramp (1985) on the other hand were from all year and probably included very few newly fledged juveniles.

Tail length

I separated adults and juveniles partly using tail measurement from studies referred to in Cramp (1985), and the difference between the studies in mean value was not very large. In my study the mean tail length was 161.7 mm for adult males and 152.1 mm for juvenile males, and 153.4 mm for adult females and 145.5 mm for juvenile females. According to Cramp (1985) the mean tail length for adult (adult and 1st adult pooled) and juveniles males is 163.5 mm and 153 mm respectively, and for adult (adult and 1st adult pooled) and juvenile females 158.5 mm and 150 mm respectively. Reasons for the small differences may be the sample sizes, since my sample was more than twice as large the ones referred to in Cramp (1985). I found a larger range than the studies in Cramp (1985) in all categories except for adult females, where Cramp (1985) had almost the same sample (20) as I had (21).

Wing length

The other morphological character than tail length that I used to determined the age of the woodpigeons was wing length, but as explained in the method my wing measurement was transformed to be compared to the ones in Cramp (1985). The differences between the mean in my study and the ones referred to in Cramp (1985) varied from ≤1-5 mm for the different groups, which would be expected when the woodpigeons were measured differently. The difference is so small that it might arise from the fact that the studies referred to in Cramp (1985) were from a whole year, whereas the samples in my study were collected over a relative short period of time.

Bill length

I found a significant difference in bill length between juveniles and adults, but not between male and female. In contrast, according to the studies referred to in Cramp (1985), there is a difference between sexes but not between the juveniles and adults. Apparently I have measured the bill length farther towards the root of the bill, than the studies referred to in Cramp (1985), because the mean bill length in Cramp (1985) was 21.3 mm compared to 28.2 mm in my study. This may explain why I found a significant difference between adult and juveniles.

Bill height

I found a significant difference between juveniles and adults, and between male and female, for bill height. The bill height in males were higher than females in this study, even the juvenile males had the same mean as adult females which indicate that this difference between the sexes starts early in the woodpigeons life. I was unable to find any studies to compare my findings on bill height.

Middle toe and length of the claw on the middle toe

I found a significant difference between juveniles and adults, and between male and female, for length of middle toe, whereas for length of claw on the middle toe I found a significant difference only between juveniles and adults. According to Cramp (1985) there is no significant difference between the sexes, and juveniles are similar to adults. I found the mean middle toe length to be 28.7 mm for males and 28.2 mm for females, and the mean length of the claw on the middle toe to be 10.3 mm for all woodpigeons in my study. According to the studies referred to in Cramp (1985), the mean toe length for males and females was 39.9 mm and 39.7 mm, respectively. There was a large gap in mean middle toe length between the studies, but if the mean middle toe length for males and females are added to the mean length of the claw on the middle toe for all woodpigeons, the mean middle toe length for males and females is 39.0 mm and 38.5 mm, respectively. Then the difference between my study and those referred in Cramp (1985) is only 0.9-1.2 mm. Considering that I obtained nearly twice as large sample as in the studies referred in Cramp (1985), and that my sample is from a short period of time right after the breeding season, the difference is small. Maybe the studies referred to in Cramp (1985) would have found a greater difference between the different sex and age groups if they had a larger sample and had measured toe and claw separately.

Net weight

In my study the mean net weight was 504.8 g for adult males and 469.5 g for juvenile males and 486.4 g for adult females and 450.0 g for juvenile females shot in August and September. Cramp (1985) refer to several studies with adult (adult and 1st adult pooled) weight or net weight. Adult male and female weight ranges 462-504 g and 480-532 g (females heaviest in May), respectively in May - October in Britain, Netherlands and Germany, and 499-526 g and 490-502 g, respectively in Scandinavia (net weight) from middle of July – December (Cramp 1985). According to Cramp (1985), the juveniles in average weigh 70 g less than the adults the first autumn. My findings support the studies referred to in Cramp (1985) when it comes to the adults, where my mean net weights are within what they found. The difference between my juvenile and adult mean net weight on the other hand (35-36 g), were only about half the difference that the studies referred to in Cramp (1985) had between adults and juveniles. Although one (Murton et al. 1974a) of the two studies on juvenile versus adult woodpigeon weight referred to in Cramp (1985) has a mean weight difference between adults and juveniles in August and September (when the sample in my study is from) on 18.5 g. From August – December the mean weight difference between adults and juveniles in Murton et al (1974a) is 39.4 g. My conclusion is therefore that also my findings on juvenile weight support earlier findings.

White neck band and weight

I found that the probability of a juvenile having the white neck band increased with its weight. The variation in weight between the woodpigeons was mainly due to the extended breeding season (Murton 1966, Cramp 1985, Slater 2001) with more than one brood raised (Haftorn 1971). Apparently the juveniles had to accumulate a certain amount of body mass before they moulted for the first time.

Flock behaviour

Age, sex and landing number in the flock

Neither of these responses was significantly affected by any of the measured variables, which is unexpected. Studies on flock behaviour in woodpigeons in winter showed that the birds in front of the flock and those feeding by themselves had significantly lower weights than those staying in other parts of the flock (Murton et al. 1971). Juveniles are often low in the social hierarchy and stay in the front of the flock (Murton 1971a, Murton et al. 1971). Birds in the front also move more around to different fields and flocks than other flock members (Murton et al. 1971). Apparently this behaviour is not important in early autumn when my samples were collected, and when there is plenty of food available and only a small part of the day is used to foraging (Cramp 1985). The flock feeding ringdove (*Streptopelia risoria*) uses knowledgeable tutors present (kin or not) to learn different feeding techniques to acquire food, but forage more often with kin than non-kin (Hatch and Lefebvre 1997).

To eat or not: flock size and body weight

Of the woodpigeons in flocks, 50% had not eaten, compared to 19% of woodpigeons in pairs and 29% of single woodpigeons. Woodpigeons use the flock as a way to locate suitable food sources (Murton and Isaacson 1962, Murton 1971b). This may explain why woodpigeons land on decoys, but not why only half the woodpigeons in flocks in my experiment had eaten. Kenward (1978) showed that goshawks (*Accipiter gentilis*) attacking woodpigeons had less success with an increase in woodpigeon flock size, which is explained by the "many-eyes" hypothesis (Pulliam 1973, Lima 1990), i.e. that as flock size increases the probability that the predator is detected by at least one individual in the flock increases in spite of that fact that each individual's vigilance time decreases (Pulliam 1973, Lima 1990). As a result the individual's feeding time indirectly increases (Elgar and Catterall 1981, Sullivan 1984, Beveridge and Deag 1987, Saino 1994, Lima 1995, Roberts 1995, Beauchamp and Livoreil 1997, Beauchamp 2004, Fernandez-Juricic et al. 2005). However, this still do not explain why only half of the woodpigeons in the flocks had eaten. It may be caused by a trade-off between vigilance and intraspecific competition. Alternatively, the woodpigeons may be in a flock since even a frontfeeding woodpigeons in a flock get more food than woodpigeons feeding in isolation (Murton et al. 1971). Note that even if the woodpigeons were shot when they were single or in pairs they were not necessarily feeding alone or in pairs. After all they were landing in a flock of woodpigeon decoys when they were shot.

Kenward (1978) showed that woodpigeons in poorer condition were more likely to be taken by the goshawk then those in better condition. This would indicate that all the woodpigeons in poor condition should have been more likely to forage in flocks to minimize the chance of being taken by a predator. However, I found no significant relation between the flock composition and woodpigeon net weight. The reason may be competition over food in the flock (Saino 1994, Robichaud et al. 1996). Alternatively, woodpigeons in poor condition forage in flocks, but not all manage to keep up with those in better condition when they fly over longer distance, and therefore are forced to fly alone from one feeding ground to another.

Temperature and time of the day had a significant effect on flock composition in my study. The reason why the probability of being in a flock was highest in the afternoon, are probably that the woodpigeons accumulate during the day on good feeding grounds(Murton et al. 1971). The reason why the probability increased with increasing temperature, are probable that the woodpigeons fly more around when the weather is good and the temperature is high. Thus, increases the possibility of meeting other woodpigeons and end up in a flock.

Diet

Eaten or not eaten different food items

I found that the woodpigeons had a varying preference for the different types of crop in my study area. Of the three types of crop for which I had a large enough sample size to do the analyzes with some certainty, barley were the least preferred both in number of woodpigeons shot in a particular field containing the crop they had eaten, and the mean dry weight of eaten fodder of the woodpigeons shot in the actual field. Wheat was the most preferred crop to land on even if the woodpigeons had eaten some fodder already. Woodpigeons shot in pea fields had the highest mean dry weight of eaten fodder. These findings support the findings from the preference index, were both peas and wheat was more preferred than barley. This may indicate that woodpigeons can recognize different types of crops from a distance and take a decision based on their condition and how much they have eaten at the time if they shall try to land and forage on the field or fly to another field with a more preferred crop further off. Earlier studies have also found differences in preference for different types of crop in woodpigeons (Murton 1965, Cramp 1985).

Oilseed rape and turnip rape

Age, middle toe length and distance to the nearest decoy from the hiding place had a significant effect on whether the woodpigeon had eaten oilseed rape and turnip rape in my study. Woodpigeons cause large damage to rape, especially oilseed rape in Britain during winter (Inglis et al. 1989, Gill et al. 1998), and the introduction of oilseed rape to Britain has resulted in lower woodpigeon mortality during winter (Inglis et al. 1994, Inglis et al. 1997). Since woodpigeons migrate from Norway in autumn (Haftorn 1971), rape has little effect on woodpigeons here during winter, although it is a preferred food item in autumn (this study and Cramp (1985)). The reason why the probability of having eaten rape was higher for juveniles than adults may be that is a high nutritive value in rape seeds, and that juveniles exploit the high fat content in the rapeseeds to put on weight. The reason why the probability increased with increasing middle toe length may be that the average woodpigeon that had eaten rape was fair-sized. The reason why the probability increased with increasing distance to the nearest decoy from the hiding-place may be that woodpigeons that have already eaten are more cautious than woodpigeons who are hungry.

Barley

Sex, age, net weight, bill height, time of day and tarsus length had a significant effect on the probability that a woodpigeon had eaten barley in my study. Earlier studies have found that barley is an important part of the diet of the woodpigeons (Folk 1984, Jimenez et al. 1994). My data show that barley is not a highly preferred food item, but since it is so widespread and cover approximately one third of the crops in my study area the woodpigeons ate it in proportion to the availability. The reason why the probability of having eaten barley was higher for males than females may be that males spend more time inside their home range and forage more on the crops available there. The reason why the probability was higher for juveniles than adults may be that juveniles are more inexperienced and more likely to eat less preferred food items such as barley. The reason why the probability increased with increasing net weight is probably that as the net weight in the woodpigeon increased in my study, so did also the chance that the woodpigeon had eaten, regardless of food type. The reason why the probability increased with increasing bill height may be spurious; I have at least no explanation for it. The reason why the probability were higher in the morning than in the evening may be that the woodpigeons had found a more preferred food item to forage on in the course of the day. Why the probability decreased with increasing tarsus length may be that the woodpigeons that forage on barley is smaller than average.

Rye

Bill height had a significant effect on the probability that rye had been eaten in my study. Rye was eaten almost tree times as often as expected from its availability. I believe this figure is too high. A reason for the assumed overestimate may be that rye is not an abundant crop in my study area. If some of the woodpigeons in my study are shot in the proximity of one or several rye fields, the fact that only 2.4% of the crop land consisted of rye would have a large effect on the preference index. Of all the studies referred in Cramp (1985), only some has found rye in their samples. This indicates that rye is not a very abundant crop in the areas were other studies has been conducted as well. The reason why the probability of having eaten rye increased with increasing bill height may be that rye seems to be a preferred foot item in my study and therefore may have a large average mean in the woodpigeons that had eaten it.

Oat

No variable had a significant effect on the probability that oat had been eaten in my study. My data suggest that oat is the least preferred crop of all. Only 7% of the woodpigeons had eaten oat in spite of oat making up almost one third of all the crops in the study area. Most of the diet studies referred in Cramp (1985) also report a low percentage of oat in the diet, if any. The reason why no variable had any significant effect on eaten oat may be that almost no woodpigeon in my study had eaten it due to the low preference for the crop.

Wheat

Vegetation type behind the hiding place, distance to the nearest decoy from the hiding place, precipitation, number of woodpigeons in the flock, wind speed, net weight and type of crop had a significant effect on whether wheat was eaten in my study. Wheat was the most preferred cereal in my study if the rye preference index is reduced (see above). A Belgian study referred to in Jimenez et al (1994) noticed a great wheat consumption in areas where barley were more abundant and both grains were equally accessible. Also Folk (1984) found wheat to be the most common food item, especially in August and September, i.e. the same time as my study was conducted. In a preference test between 12 different food items, wheat was one of the four most preferred by woodpigeons (Murton 1965, Cramp 1985). One reason why the probability of having eaten wheat decreased with increasing height of the vegetation type behind the hide may be that since the woodpigeon already had eaten a preferred food item like wheat (Murton 1965, Cramp 1985), it would not be compelled to take the chance of landing to close to high vegetation that can hide a potential predator. The reason why the probability decreased with increasing distance to the nearest decoy from the hide, may be that woodpigeons that had eaten wheat in my study to a larger extent landed beside decoys located in the proximity of low vegetation, which has a smaller chance of hiding a potential predator. Thus the woodpigeons could take the chance of landing beside decoys closer to the edge of the field. The reason why the probability was highest with little precipitation and lowest with some precipitation, may be that before a bad weather starts the woodpigeons try to eat as much as possible (pers. obs.). When the precipitation intensity increases the woodpigeons will probably not forage as effectively, and therefore would have eaten less with some precipitation in my study. The reason why the probability was highest with pigeons in pairs and lowest with pigeons in flocks, have been discussed above. The reason why the probability was highest with fair wind and lowest with weak or strong wind, may be that woodpigeons fly very well (pers. obs), and exploit the wind to their advantage, but when the wind is weak or very strong the woodpigeons may not manage to exploit the wind to their benefit. The reason why the probability increased with increasing net weight is probably that as the net weight in the woodpigeon increased in my study, so did also the chance that the woodpigeon had eaten, regardless of food type. The reason why the probability was highest in wheat fields and lowest in barley fields, may be that since they already had eaten a preferred food item like wheat, the woodpigeons had a higher chance of landing on a preferred crop than a non-preferred one.

Pea

Wind speed, vegetation type behind the hiding place, date and net weight had a significant effect on whether peas had been eaten in my study. Peas had definitely the largest preference index of all the crops. Although this preference is somewhat overestimated in my opinion, peas are nevertheless a highly preferred food item (Murton 1965), and in my opinion the most preferred crop by woodpigeons in Norway. Reasons why the preference index was overestimated is probably that a large part of the woodpigeons were shot at or in the proximity of some of the few fields with peas in my study area. In a preference test between 12 different food items, peas were one of the four most preferred by woodpigeons (Murton 1965, Cramp 1985). Since peas are not a common crop in my study area; but a preferred one, woodpigeons sometimes accumulate in areas with one or several pea fields and form occasionally very large foraging flocks (pers. obs). Several studies referred in Cramp (1985) also found that peas were an important food item, especially at times of the year when they were most accessible to the woodpigeons. A reason why the probability of having eaten peas was highest with strong wind and lowest with fair wind, may be that there are often many woodpigeons in the proximity of pea fields (pers. obs.), and in strong wind conditions they may fly only to the nearest field, but in fair wind conditions they may fly longer distances and with that to a larger extent ending up foraging in other crops than peas. The reason why the probability was highest when vegetation type behind the hide were minor trees, may be that a lot of the woodpigeons shot in the proximity of pea fields, were shot when the vegetation type behind the hide consisted of minor trees. The reason why the probability decreased as the days went by during the study period may be that peas are harvested early in the season (pers. obs.). The reason why the probability increased with increasing net weight, are probably that as the net weight in the woodpigeon increased in my study, so did also the chance that the woodpigeon had eaten, regardless of food type.

Grit

Only net weight had a significant effect on whether grit was eaten in my study. Type of crop was not anticipated to have a significant effect on eaten grit or not, because grit is found everywhere and woodpigeons often eat grit in e.g. gravel roads (pers. obs.). Number of woodpigeons in the flock did not affect whether grit had been eaten, which indicates that woodpigeons probably do not depend on flock members to find grit since it is so abundant in contrast to what is the case for food. Grit-ingesting birds need grit to help them with their digestion (Bendell-Young and Bendell 1999), and it is rather remarkable that some other studies have found very little grit in the crop (Jimenez et al. 1994). Jimenez et al (1994) found only 5 grits in total in the crops, and although their study was based on a smaller sample than mine, this is unlikely to be the explanation. Their sample was almost exclusively from the morning, while mine was from both morning and evening, however since the distribution in eaten grit was nearly even between morning and evening in my study this is hardly the explanation either. In addition, a study referred to in Cramp (1985) reports that grit was often collected from roads in early morning. Grit searching is also most common in the grain season, presumably because seeds require more grinding than leaves (Murton 1965, Cramp 1985). The reason why the probability of having eaten grit increased with increasing net weight, are probably that as the net weight in the woodpigeon increased in my study, so did also the chance that the woodpigeon had eaten, regardless of food type or in this case grit.

Various wild seeds and leaves (pooled)

The length of claw on the middle toe, bill length, bill height, vegetation type behind the hiding place, wind speed, type of crop, number of woodpigeons in the flock, distance to the nearest decoy from the hiding place, and precipitation had a significant effect on whether native vegetable matter had been eaten in my study. The quantity of various wild seeds and leaves in the crops was low, e.g. often only a single seed in a crop. Only one crop contained some quantity of wild seed (2.5 g), but the species was sunflower which may be grown in a few small patches within the study area, especially in gardens. Earlier studies have also found that only a few woodpigeons fed on sunflower, but those who did often consumed large amounts of these seeds (Folk 1984, Jimenez et al. 1994). All together, earlier studies have found that wild seeds are of little importance to the woodpigeon's diet in the period of the year when my study was conducted (Murton 1965, Folk 1984, Jimenez et al. 1994), up to 17% of the diet, but in most studies less than 2% (Jimenez et al. 1994). The reason why the probability of having eaten wild seeds and leaves increased with increasing length of claw on the middle toe, decreased with increasing bill length, increased with increasing bill height, increased with increasing wind speed, and were lowest with some precipitation are probably spurious because much of the wild seeds and leaves in my study I believe was eaten by mistake or random since they consisted only of one item in many samples. The reason why the probability were highest in wheat fields and lowest in barley fields, and were highest in pairs and lowest in flocks, have been discussed above. The reason why the probability decreased with increasing distance to the nearest decoy from the hide, and was highest with lowest vegetation type behind the hide, has been discussed above. Alternatively, it can indicate that those woodpigeons that had eaten wild seeds and leaves preferred to stay closer to the edge of the field in places were the vegetation was low and wild seeds and leaves more abundant.

Various animals (pooled)

Wind speed, type of crop, distance to the nearest decoy from the hiding place, vegetation type behind the hiding place, time of day, precipitation, net weight and date had a significant effect on whether animals had been eaten by the woodpigeons in my study. There was a tendency that more woodpigeons had animals in their crop in the start of my study period, and that the portion of animal food in the crop decreased as the days went by. Most of the woodpigeons that had eaten animals in my study had only one type of animal in their crop. No woodpigeons had eaten >1 g of dried animal matter in my study, so it would be an overstatement to say that animals were an important part of woodpigeon diet when my study were conducted. Most of the animals matter in the crops was snail remnants which dissolve slowly. Earlier studies have pointed out that animal matter in woodpigeon crops dissolves quickly (Folk 1984). Animals may then be overlooked in diet studies based on the gizzard, but also the crop (Folk 1984). Several earlier diet studies on woodpigeons have, as a consequence of this, found no animal content (Cramp 1985, Jimenez et al. 1994), and several others only a small part of animals in the diet of the woodpigeon (Murton 1965, Folk 1984)and several studies referred to in Cramp (1985)). The reason why the probability of having eaten various animals was highest with strong wind and were lowest with fair wind, was highest on wheat fields and lowest on barley fields, increased with increasing distance to the nearest decoy from the hide, was highest with lowest vegetation type behind the hide, was highest in little precipitation and lowest in some precipitation, and increased with increasing net weight, have been discussed above. The reason why the probability was higher in the morning may be that most of the animals that had been eaten by the woodpigeons were snails which like the morning dew. The reason why the probability decreased as the days went by, may be that the animals that the woodpigeons hade eaten in my study is less active during autumn.

All crops and all food items (pooled)

Number of woodpigeons in the flock, type of crop and net weight had a significant effect on whether any crop, or any food, had been eaten in my study. The 72 woodpigeons that had eaten at least one type of crop had from 1-9 different food items in their crop. Of the fodder 94.4% came from crops, 0.8% from other plant material, 0.6% from animals, and 4.2% from grit. Earlier studies from early autumn have also found mostly seeds from crops in the diet of woodpigeons (Murton 1965, Folk 1984, Cramp 1985, Jimenez et al. 1994). Jimenez et al (1994) found 17 different plant species in their study, whereas I found 18. Among the 72 woodpigeons, 21% had only one type of item in their crop, and 61% had more than two (maximum nine). In comparison, in a study from Sweden referred to in Cramp (1985), 31% of the woodpigeons had one species and 46% had more than two different species in their crop (maximum seven). Considering the possibility that the Swedish study (Cramp 1985) did not include grit (since it reported species and not items) and covered a longer period (Cramp

1985), the differences between the two studies are negligible. Folk (1984) suggested that the woodpigeons mainly consume two types of seed in the season my study was conducted; cereal grains and round seeds (represented mainly by peas, vetches and rape), thus the woodpigeon could be considered a granivorous bird in summer (Jimenez et al. 1994) and early autumn. For the following crops the sample was large enough to allow calculation of the portion of the shot woodpigeons that had eaten when they were shot in pea, wheat or barley fields, respectively. The result may indicate that if the woodpigeons had not eaten at all or only eaten a small amount, they may have landed in all sorts of fields that had other foraging woodpigeons, also less preferred ones such as barley. On the other hand, if they had eaten some food already, the probability of landing in anything but a preferred field of food decreased. As a woodpigeon's net weight increased in my study, the probability that the woodpigeon had eaten also increased. This may indicate that the reason why that woodpigeons are in good condition are because of their abilities to find food. Murton et al (1971) found that subordinate woodpigeons obtained food of poorer quality than the average woodpigeon in the flock and had less pecks per minute than the dominant woodpigeons. Woodpigeons in poorer condition are more likely to get shot since they move more than dominant flock members (Murton et al. 1971), and are more easily caught by a predator (Kenward 1978).

Conclusion

My most important findings were that the first moult of the juvenile woodpigeons depended on their body mass. As the net weight increased the probability that a woodpigeon had eaten increased. Moreover, the percent of woodpigeons that had eaten depended on whether they travelled alone, in pairs or in a flock. The woodpigeons did not eat different types of crop according to the availability of the crop, but rather ate different crops depending on body condition, and how much food they had eaten at the present time versus how preferred the crop in question was. Further studies should look into how long woodpigeons are willing to fly to get to a preferred food source, how condition affects the flight distance, and investigate why only half of the woodpigeons flying in flocks had eaten.

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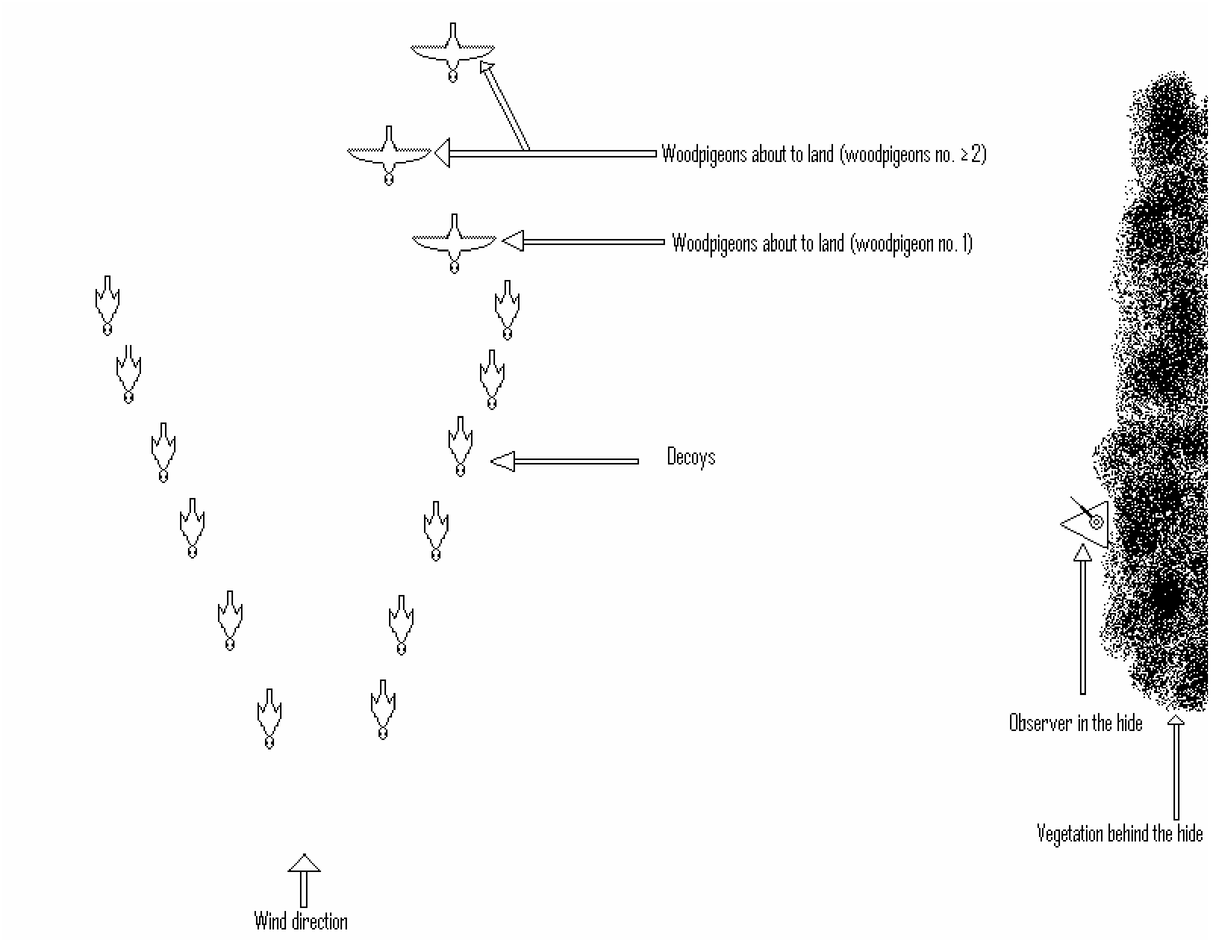
Appendix 1


Woodpigeons about to land (woodpigeons no. ≥ 2)
Woodpigeons about to land (woodpigeon no. 1)
Decoys
Observer in the hide
Vegetation behind the hide
Wind direction