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FOOD DISTRIBUTION AND A VARIABLE MATING SYSTEM IN THE DUNNOCK, *PRUNELLA MODULARIS*

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SUMMARY

(1) The mating combinations were very varied and included monogamy (pairs), polyandry (two or three males with one female), polygyny (one male with two females) and polygynandry (two or three males shared two, three or four females).

(2) Female ranges were always exclusive. Where two or three males shared one or more females, the ranges of the males overlapped and they cooperated to defend the territory. There was a dominance hierarchy among the males; alpha males were often old birds and beta males often first year birds. There were no known cases of close relatives being involved within any of the mating combinations.

(3) It is suggested that the different mating combinations form a continuum in a male's ability to monopolize access to females, varying, in increasing order of mating success, from unpaired, to shared access to one female (polyandry), sole access to one female (monogamy), shared access to more than one female (polygynandry) and finally sole access to more than one female (polygyny).

(4) The ability of a male to control access to females depended on female range size, which was influenced by food distribution. Where food patches were dense, female ranges were small and they were then easily monopolized giving rise to mating combinations that reflected high male mating success (polygyny and polygynandry). Where food patches were sparse, female ranges were large and they were difficult for one male to monopolize, thus giving rise to mating combinations with lower male mating success (polyandry).

(5) When extra food was provided on some territories, female ranges became smaller and the mating system shifted towards greater male mating success (from polyandry towards monogamy and polygynandry).

INTRODUCTION

In many species a female's reproductive success is limited by her access to resources whereas a male's reproductive success is limited by his access to females (Darwin 1871; Trivers 1972). Mating systems, therefore, should often be related to the ability of males to control access to females. The degree of control will depend on two main factors (Emlen & Oring 1977). Firstly ecological conditions such as the dispersion of food, nest sites and predators will influence female distribution which, in turn, will determine their economic defendability by males. Secondly, the ability of males to monopolize females will depend on the amount of competition for mates at any one time, which will be reflected by the operational sex ratio (the local ratio of receptive females to sexually active males).

Three main methods have been used to test these ideas. The comparative approach across different species has shown that, as predicted, differences in mating systems are

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linked to resource dispersion and the temporal availability of mates (e.g. primates, Clutton-Brock & Harvey 1977; Wrangham 1980; ungulates, Jarman 1974; birds, Crook 1964; Verner & Willson 1966; frogs, Wells 1977; Arak 1983). Observations of variations within a species have likewise shown a correlation between a male's mating success and his ability to control access to females or resources that the females require (e.g. nest sites, Verner 1964; Pleszczyńska 1978; food, Wittenberger 1980). The third method, experimental manipulation of the factors supposed to influence the mating system, has been rarely used.

Two experiments have tested directly the idea that resource distribution influences polygyny. Pleszczyńska & Hansell (1980) increased the number of females in male lark bunting (*Calamospiza melanocorys*) territories by providing extra nest sites while Ewald & Rohwer (1982) did likewise for male red-winged blackbirds (*Agelaius phoeniceus*) by the provision of extra food. One experiment has investigated the importance of mate competition. By removing males from a population, Smith, Yom-Tov & Moses (1982) showed that the operational sex ratio can influence the mating system of song sparrows (*Melospiza melodia*), a typically monogamous species; the degree of polygyny increased because the widowed females formed associations with already mated males.

Here we describe observations and an experiment to investigate the ecological factors that influence the mating system of the dunnock (or hedge sparrow, *Prunella modularis* L.). The species is of unusual interest because it has a very variable mating system with monogamy, polygyny, polygynandry and polyandry often all occurring together within the same population (Birkhead 1981; Karanja 1982; Snow & Snow 1982; Davies 1983). This variability provides a good opportunity to explore the eco-correlates of mating systems and to test by experiment how changes in ecological conditions can influence females' dispersion and their defendability by males.

STUDY AREA AND METHODS

The study area is the Cambridge University Botanic Garden, an area of 16 hectares which includes a diversity of habitats. There are areas of woodland with dense undergrowth, open woodland with little undergrowth, hedgerows (mainly hawthorn *Crataegus* and evergreens *Taxus*, *Thuja*), flowers beds, shrubs, long grass, dense patches of giant hogweed (*Heracleum mantegazzianum*) and areas of open lawn. The result is a patchwork of different vegetation types and densities which provides an ideal natural experiment for observing on a small scale how habitat influences bird distribution.

The dunnock population has been studied since October 1980. In the first breeding season, 1981, an area of 7.7 ha was studied but in subsequent years the study area has included the whole garden. Almost all of the birds were individually recognizable by colour rings (forty-five out of the forty-nine breeding adults in 1981, seventy-two out of seventy-seven in 1982 and eighty-one out of eighty-six in 1983). Most of the nests were built in hedges and evergreen bushes and were easy to find. All the nestlings were colour ringed (forty-five in 1981, 116 in 1982 and 159 in 1983). Some remained to breed in the garden but many disappeared soon after independence, presumably dispersing to other areas. In late summer and autumn there was an influx of young birds born outside the study area. Some remained to breed the next summer but many left after a brief visit. These immigrants were easily recognized by their pale legs and dark brown eyes (adults have red-brown eyes) and were also colour ringed (forty-two in 1981, thirty-six in 1982). Wing lengths were measured from the carpal joint to the tip of the longest primary, with the wing closed and pressed flat against a rule held along the long axis of the bird's body. Tarsus lengths were measured, with vernier callipers, from the notch in the angle of the intertarsal

joint to the tip of the bended foot. This measure is slightly larger than the true tarsus (Svensson 1970) but it is easier to take and more repeatable. Females were easily distinguished from males both by plumage (females were less grey on the head and underparts) and behaviour (females very rarely sang, males did not incubate and the difference in behaviour during copulation was very distinctive; Davies 1983).

Transects were made daily in the breeding season and two–five times a week in the winter and the positions of individuals were marked on a map. Range areas were calculated by the maximum polygon method (Odum & Kuenzler 1955) and male song territories were calculated as the area within the maximum polygon drawn around the male's regular singing perches. Occasionally birds wandered a long way outside their territories (e.g. to drink at a pond) and these map registrations were ignored when the maximum polygons were drawn. Most adults were sedentary and the boundaries of their regular home range were easy to draw. Continuous watches were made of individuals for periods of 10–60 min to record time budgets; activities were categorized into time spent feeding, perching (including song), preening and interactions with others.

In both 1982 and 1983 we put out food on ten randomly chosen territories to investigate the influence of extra food on time budgets and ranges. In each territory, food was placed in and around a wire mesh cylinder about 35 cm in diameter and 30 cm in height. This prevented the more aggressive robins (*Erithacus rubecula* L.) from monopolizing the food because the wire mesh acted as a barrier that enabled several birds to use the feeder at the same time. The most frequent users of the food were dunnocks, robins and starlings (*Sturnus vulgaris* L.). In 1982 the food consisted of a mixture of porridge oats, bread crumbs, maggots and mealworms and it was put out daily early in the morning, from 15 January to 15 May. In 1983 Haith's softbill food mixture (consisting of insects and seeds blended with honey and vegetable oil) was put out daily from 7 January to 14 July.

RESULTS

Sex ratio in the breeding population

The sex ratio of adults was male biased in each breeding season with male:female ratios of 1.13 in 1981, 1.48 in 1982 and 1.26 in 1983 (Table 1). This imbalance was almost certainly due to greater female mortality, particularly in winter. Survival of adults was scored from 1 April to 1 April the next year so that the whole of a winter was included in one survival year (following Snow & Snow 1982). Twenty out of twenty-six males (76.9%) present on 1 April 1981 survived to 1 April 1982 compared with only six out of twenty-one females (28.6%; $\chi^2 = 9.11$, d.f. = 1, $P < 0.01$). This probably reflects a difference in survival and not simply movement out of the study area because both males and females are sedentary breeding on almost exactly the same territories from year to year. Females are smaller than males and subordinate at feeding sites, and much of the female mortality occurred in the 1981–1982 winter which was very cold (see also Birkhead 1981; Snow & Snow 1982). The following winter, 1982–1983, was very mild and there was no sex difference in survival; thirty out of forty-six males (65.2%) survived from 1 April 1982 to 1 April 1983 compared with sixteen out of twenty-seven females (59.2%). As a result, the sex ratio in the 1983 breeding season was not as male-biased as in 1982.

Description of the different mating combinations

The enormous variety in mating combinations of the dunnock appear at first bewildering and complex (Table 1). There was polyandry (two or sometimes three males associating with the same female), monogamy (simple pairs), polygyny (one male with two females)

TABLE 1. Mating combinations at the start of the breeding season for 3 years

Mating combination	Frequency			Total
	1981†	1982*	1983*	
Unpaired ♂	1	1	3	5
Polyandry 3♂♀	—	1	1	2
2♂♀	4	12	8	24
Monogamy ♂♀	13	11	10	34
Polygyny ♂2♀	2	—	—	2
Polygynandry 3♂2♀	—	1	—	1
2♂2♀	1	1	6	8
2♂3♀	—	1	1	2
2♂4♀	—	—	1	1
Breeding population				
No ♂	26	46	48	
No ♀	23	31	38	

* Includes territories with artificial feeders—see later.

† Only part of the garden was studied in 1981 (see Methods) and so the absolute population size cannot be compared directly with the other 2 years, when the whole garden was studied.

and polygynandry (two or three males sharing access to two, three or four females). In all 3 years, the commonest mating combinations were monogamous pairs and associations between two males and a female, which we call 'trios'.

There were three features common to these mating systems.

(i) Female ranges were largely exclusive (Fig. 1). Thus where a male had two females, each occupied a separate range within his territory (Fig. 1c). Similarly, where two males

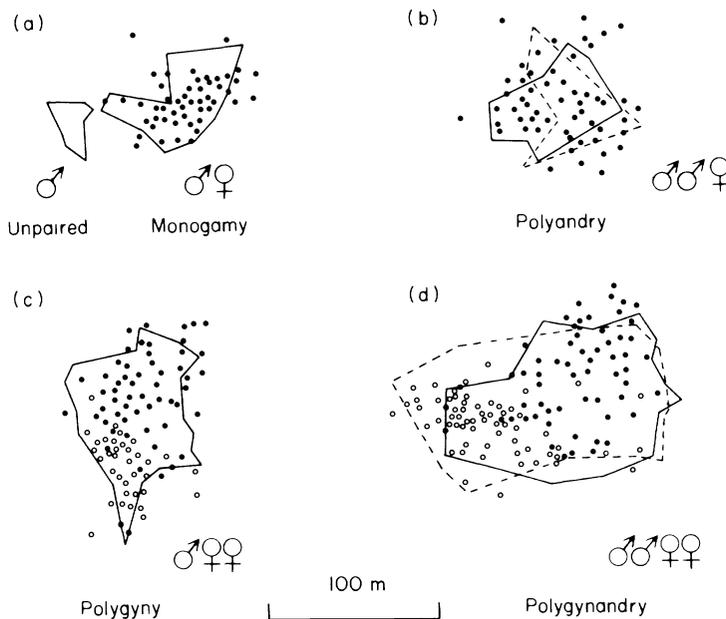


FIG. 1. Examples of the different mating combinations. (—, ---), Male song polygons; female ranges, (●, ○), each point representing a first sighting during a transect around the study area. Female ranges are largely exclusive but when two males share one or two females, their song polygons overlap.

shared access to two females each female again had a separate range and the ranges of both males overlapped both the females (Fig. 1d). Females were aggressive to other females and there were chases and occasionally serious fights at their range boundaries.

(ii) There were no known cases of close relatives being involved within any of the mating combinations. The origins of the females were known for eight of the twelve cases of polygynandry. Six of these involved two females living as neighbours within the range of two males, and all six were cases of old females, who had bred previously on the same territory, with young females next door who were definitely not their previous offspring. Four of the young females were immigrants to the study area, born outside the garden, while two were born in the garden the previous year, one coming from five female territories away and the other from four female territories away. In one case of three males plus two females, one of the females was an old female and the other was a first-year immigrant. In one case of two males plus three females, one of the females was an old female, one a young immigrant and the other a young bird born six female territories away in the garden the previous year. It is clear, therefore, that young females disperse from their natal territories and are not likely to be involved in polygynandrous associations with close relatives.

Likewise none of the males within the same mating combination were close relatives. The origins of the males were known in eight cases where two males shared the same female. Six cases involved an old male plus an immigrant first year male and two involved an old male plus an unrelated first year male born on the study area. One of these young males came from two territories away and the other from three territories away. The origins of the males were known in five cases where two males shared two or three females. Three cases involved an old male plus a young immigrant male while two cases involved an old male plus a young male born in the garden, one from three territories away and one from four territories away.

(iii) Whenever two males shared one or more females there was usually a clear dominance order, one male (the alpha male) displacing the other (the beta) from food patches and from females. Where three males shared one or more females, there were clear alpha, beta and gamma males. Alpha males had longer wings than beta males (Table 2). Wing length is not a good measure of body size, however, because it changes with age. Taking all measurements in all years of males breeding in the garden, first-year males had significantly shorter wings (mean \pm S.D. = 69.06 ± 1.22 , $n = 33$) than males of 2 years or older (mean 70.83 ± 1.50 , $n = 18$, 2-tailed t -test, $P < 0.001$). A similar result is obtained with a matched comparison of nineteen males who were measured in both their first and second breeding seasons (mean wing length first year = 70.31 , second year =

TABLE 2. Measurements of males. Figures are means and one standard deviation with sample size in brackets. There was one significant difference, t -test, 2-tailed

Mating status	Wing length mm	Tarsus length mm
Monogamous males (σ^2)	71.00 ± 1.49 (18)	21.26 ± 0.85 (11)
Polyandrous males ($2\sigma^2$)		
alpha male	70.75 ± 1.20 (20)	21.45 ± 0.76 (19)
beta male	69.44 ± 1.38 (25)*	21.35 ± 0.67 (20)

* $P < 0.01$.

70.84, Wilcoxon matched pairs test 2-tailed, $P < 0.01$). A better measure of body size is tarsus length, which does not change with age, and there were no significant differences between alpha males, beta males or monogamous males in this measurement (Table 2). The wing length difference between alpha and beta males, therefore, is probably simply a reflection of age rather than body size. In support of this idea, considering only males of known ages, eleven out of seventeen beta males in trios were first year birds compared with only two out of eleven alpha males ($\chi^2 = 4.09$, d.f. = 1, $P < 0.05$).

Changes within a breeding season

There are not enough data to show how individuals change mating status with age because most of the territories were affected by the feeder experiments (see later) and this confounds the interpretations. However, the alpha-beta dominance between two males was not always a permanent rank order. In three of the eight cases where two males shared one or more females in successive years, the ranks reversed in the second year. In one of these cases a male was beta male to an old male (2 years or more) in this first year but then became alpha male the next year. The ages of the males in the other cases were not known. In one territory following a serious fight between them, the rank order of the males reversed between the first and second broods of a breeding season.

Table 1 gives the mating combinations at the start of the first broods each year. However, within a breeding season there were often changes due to movements and mortality. These are summarized below.

(a) Five females died early in the breeding season. In three cases they had been paired monogamously and all three males joined neighbouring monogamous pairs as beta males of trios. In the two other cases the female had been paired to two males. In one case the alpha and the beta male each forced themselves onto different neighbouring monogamous pairs as beta males of trios. In the other case, the beta male disappeared and the alpha male joined a neighbouring trio as a gamma male.

(b) Two monogamous males died and in both cases a beta male left a neighbouring trio and claimed the female, forming a monogamous pair.

(c) Seven alpha males of trios died. In five cases the beta male took over as a monogamous male for the rest of the breeding season. In the other two cases another male arrived and became a beta male, with the original beta male becoming alpha male of the new trio.

(d) Eight beta males of trios died. In five cases the alpha male took over as a monogamous male and in three cases another male arrived as a new beta male.

The summary of the mating combinations in Table 1 is further complicated by the fact that males whose females are busy incubating will sometimes trespass next door and attempt to mate with neighbouring females who are at the egg laying stage. These trespassing males are chased off by the residents but they are often persistent in their pursuit of the female especially around the territory boundaries.

There is, fortunately, a simple hypothesis to explain this great variability in the mating system within the same population. The different mating combinations may simply form a continuum in a male's ability to monopolize access to females. The rest of the paper is an attempt to test this hypothesis.

The setting up of male song territories in spring

During the winter, dunnocks fed solitarily on small seeds and invertebrates. From two to six individuals shared overlapping home ranges and sometimes they all congregated

temporarily at rich feeding patches within the range. If the weather was not too cold, then in late January and throughout February and March the males began to set up exclusive singing territories within their winter feeding ranges. At first, a male tolerated the presence of other males feeding within his song territory but if they sang then they were chased. Later, all trespassing males were chased from the song territory whatever they were doing.

The size of a male's song polygon in late winter and early spring was quite a good predictor of his future mating status (Fig. 2). Unpaired males had the least mating success.

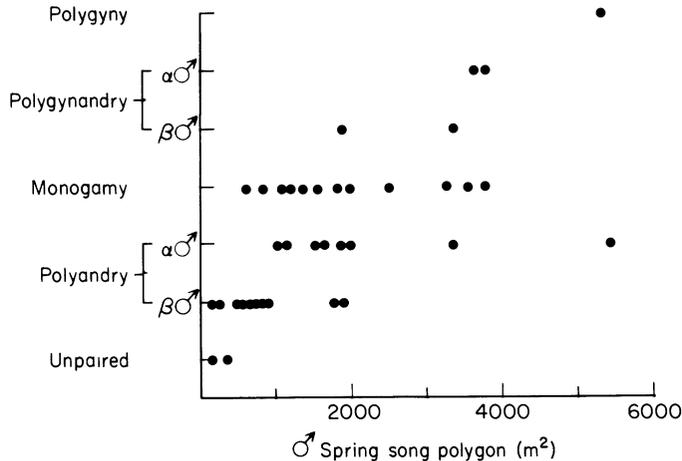


FIG. 2. Males with larger song polygons have greater mating success. Spearman rank correlation, corrected for ties, = 0.641, $P < 0.01$. The different mating combinations have been ranked up the y axis in increasing order of male mating success. Spring song polygons were measured in February and early March before any coalescence of male territories had occurred (see text). Males with feeders are excluded from this analysis (see later).

Within trios two males shared copulations with the one female and the beta males were less successful than the alpha males (Davies 1985). Monogamous males had exclusive mating access to their female and so were more successful than either of the trio males. In polygynandrous associations, the matings were again shared unequally with the alpha male performing more than the beta male. In cases where two males shared two females, therefore, the beta male may have lower mating success than a monogamous male (less than half the matings with each of two females compared with all the matings with one female). The alpha male, however, will usually do better than a monogamous male. In cases where two males share more than two females, mating success for both alpha and beta male may be greater than for monogamy. Finally, the most successful males were polygynous males who had sole mating access to two or more females. The relationships between a male's reproductive success and the mating system will be analysed in another paper, but for the purposes of the present analysis it is clear that mating success, measured as the number of females a male can monopolize, increases with the size of his song territory. There was no correlation between a male's tarsus length and the size of his song polygon ($r = 0.159$, N.S., $n = 21$) and therefore no indication that larger males defended larger song polygons.

Female ranges in spring and formation of different mating combinations

In early spring, males often chased females for continuous periods of up to 10 min.

During these chases the female would sometimes fly around the whole of her range pursued by the male who followed her every move, twisting and turning through the vegetation. Whenever the female perched for a short period on a branch the male sat by her and occasionally sang, but as soon as she flew off again he followed closed behind. These sexual chases gave the impression that the male was learning the details of a female's range and attempting to set up a song territory around her.

Some females ranged solely within the singing territory of one male and these then formed monogamous pairs for the breeding season. Other females, however, wandered over the song territories of two neighbouring males (Fig. 3). Whenever this happened, each male attempted to follow the female when she crossed the boundary into the other male's territory. Chases occurred and at first the dominance order of the two males would reverse as they crossed into the other's song polygon, with each resident being dominant on his own territory. However, after several days of chasing and song duals, with both males pursuing the female over the whole of her range, a clear dominance order would emerge between the males and both would then sing over the whole of the female's range (Fig. 3).

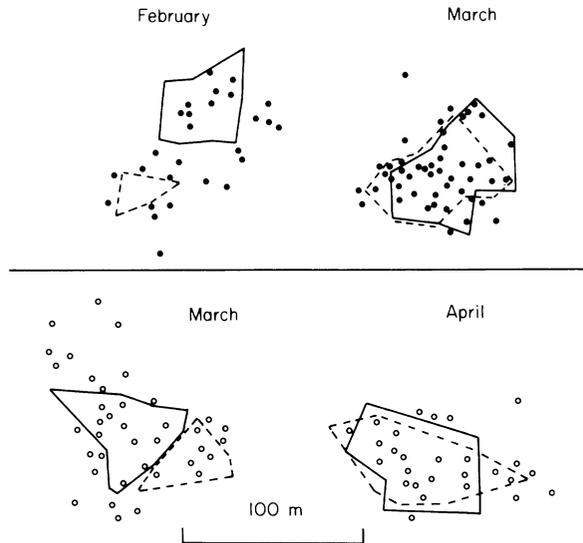


FIG. 3. Two examples of trio formation by the coalescence of two neighbouring male territories. In each case two males have separate song territories in early spring, denoted by solid and dashed lines. A female spends time in both male territories, the solid or open circles representing the first sightings of the female on transects around the study area. By late spring the two males have coalesced their territories and they have overlapping song polygons and share the female.

The result, therefore, was that the two neighbouring males coalesced their territories and came to share the same female as alpha and beta male of a trio. Once territory coalescence had occurred, both males shared song perches with little aggression between them and they often defended the territory together by displaying as a team against neighbouring males. Although the two males apparently come to agree to share the territory in this way, conflict between them starts up again once the female begins to lay eggs reflecting disagreements over how the copulations should be shared (Davies 1985).

Sixteen cases of trio formation were followed in detail at the start of the breeding season. Fourteen of these formed by the coalescence of two neighbouring male song territories

when a female ranged over both their areas. In the two other cases the trio formed in a different way. Some first year males wandered around the whole of the study area in early spring, singing briefly and were then evicted by the resident male from each territory in turn. Some of these males left the study area but two managed to force themselves onto territories where there was a monogamous pair. The resident male chased the newcomer but over a period of several days the chases decreased as it persisted and it was eventually accepted on the territory as a beta male. One of the wandering males spent 19 days roaming around the study area and was seen attempting to settle on nine different territories before it was finally accepted on one, while the other male spent 4 days wandering and was seen to be evicted from five territories before it managed to settle on another. Later on in the breeding season, when mortality caused changes in the mating combinations several trios formed in a similar way to this when bereaved males forced themselves onto other territories and were accepted as subordinate males (see above).

One case of the formation of three males plus one female was followed in detail and this involved a female wandering over three male song territories in early spring, and then the subsequent coalescence of all three territories with the three males sharing the whole range as alpha, beta and gamma. Most of the examples of polygynandry were a result of the feeder experiments (see later) but one was studied which formed naturally. Here there were initially two neighbouring monogamous pairs. One of the males then began to sing over the neighbouring male's range as well as his own. He met with little resistance and after a few days he became alpha male over both female ranges with the other male becoming beta over both ranges.

The influence of food distribution on female ranges and the mating system

It is clear that females are not constrained in their movements by male territory boundaries when they set up their ranges in spring. The behaviour involved in sexual chases and the way that trios form by coalescence of neighbouring male territories suggest that a female decides on her range and males then have to compete to monopolize that range. This is in marked contrast to many birds where a male first sets up a territory and a female then settles within its boundaries. For example, in robins a female settles on a male's territory in early spring and she then follows him around, apparently learning the territory boundaries which will restrict her range (Harper 1984). This is the reverse of the dunnock, where the male follows the female.

The next question, therefore, is what determines the female's range size? The most likely hypothesis is that it depends on food distribution. Dunnocks are ground gleaners which pick up tiny seeds and invertebrates, and they usually forage in dense vegetation. In the Cambridge Botanic Garden they spent almost all their time feeding in flower beds, usually in thick cover, and at the base of trees and under dense bushes. These good foraging areas were distributed as patches of different sizes and densities amongst more open areas of lawn that were rarely used for feeding. Figure 4 shows that female ranges were largest in areas where there was a low density of suitable foraging patches and smallest where most of the range consisted of dense vegetation and flower beds. Snow & Snow (1982) also reported qualitatively that ranges were smallest in 'good habitat'. Furthermore, the points in Fig. 4 give a rough approximation to the expected curve if female range size was adjusted so that each contained the same average feeding area.

The consequence of a female's total range size for her ease of monopolization by males is shown in Fig. 5. It is clear that the larger the female's range, the more likely she is to associate with more than one male. The mean range size for monogamous females was

Dunnock mating systems

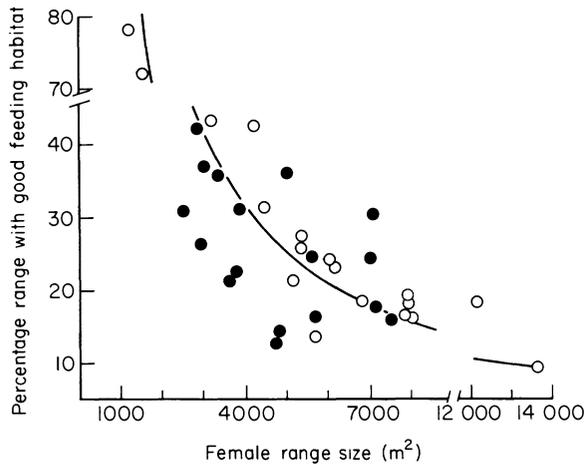


FIG. 4. Females ranges are largest in poor feeding areas. (●), Data from 1981; Spearman rank correlation = -0.526 , $n = 17$, $P < 0.05$. (○), Data from 1982 (excluding feeder territories), Spearman rank correlation = -0.873 , $n = 18$, $P < 0.01$. The curve drawn through the points is the expected curve if all females had the same feeding area within their range, namely the average area of flower beds and bushes in female ranges, which was 1269 m^2 . Note the breaks in both axes.

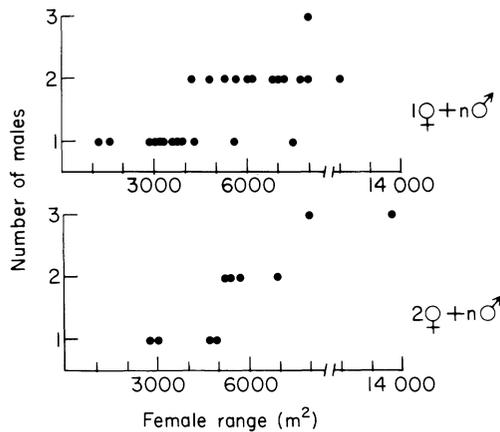


FIG. 5. The larger a female's range, the more likely she is to associate with more than one male. The top graph plots cases where one female associated with one male (monogamy) or two or three males (polyandry). The bottom graph plots the ranges of each female where the mating system was two females associated with one male (polygyny) or two or three males (polygynandry). Females with feeders are excluded from this analysis (see later).

3625 m^2 ($n = 12$) which is significantly less than that for biandrous females (mean 6759 m^2 , $n = 12$, Mann-Whitney U -test, 2-tailed, $P < 0.002$). The fact that females who are monopolized by two males have, on average, twice the range size of those monopolized by one male is what would be expected if trios were formed by coalescence of two male territories with two males being able to defend twice the area of one male.

Feeder experiment

The observations above support the hypothesis that a female's range is influenced by

food distribution and the size of her range then determines the mating system through her ease of monopolization by males. The hypothesis was further tested by the provisioning of extra food (see methods). We predicted that, with extra food, a female's range would be smaller and she would then be more easily monopolized by one male. As a result the mating system was predicted to shift from polyandry towards monogamy.

The influence of provisioned food on range size

In both years of the feeder experiment, the feeders were placed approximately in the centre of ten randomly chosen female ranges but there followed changes in the boundaries of the ranges. In 1982, twelve females had regular access to the ten feeders; eight had sole access to feeders in the centre of their ranges while the other two feeders were on the boundaries of two neighbouring female ranges and were each used by two females. In 1983, sixteen females had regular access to the ten feeders; five feeders were in the centre of one female's range, four were on the boundaries of two neighbouring females and were used by both and one feeder was on the boundary of three female's ranges and was used by all three females.

Birds with feeders quickly came to use the provisioned food and it had a marked effect on their time budgets compared to control birds (Davies & Lundberg 1985). In February and March, before nest building began and during the period the males were competing to set up song territories, the females spent on average 23.5% of the day feeding at the feeder (range 5.2–41.7%; data from eleven feeder females in 1983). They spent on average 36.4% (range 6.2–75.0%) of their total daily foraging time feeding on the provisioned food and so this formed a major source of their daily food intake. The equivalent figures for use of the feeders by males who had feeders within their ranges were an average of 16.5% (range 4.8–34.6%, $n = 16$) of the day spent feeding at the feeder and 48.6% (range 19.6–77.8%) of the total daily foraging time spent feeding on the provisioned food.

As predicted, females with feeders had smaller ranges than females without but the feeders had no significant effect on male range size (Table 3a). Some birds were present in both years of the experiment and had feeders in one year but not the other. Four females had feeders in 1982 but not 1983 and six had feeders in 1983 but not in 1982. All ten

TABLE 3. (a) Territory sizes of male and female dunnocks in control and feeder territories. Data for 1982 and 1983 combined. Significant differences with 2-tailed Mann-Whitney U -test. Figures are means \pm 1 S.E., with sample size in brackets (b) Matched comparisons of territory size of the same birds on the same territories in 1982 and 1983, but with food in only one year. Wilcoxon matched pairs test, 2-tailed. Not sufficient data to test single males

(a)	Territory size m ²	
	Feeder	Control
Females	2776 \pm 379 (28)	4572 \pm 476 (39)*
Males		
territories defended by one male	2864 \pm 340 (11)	2642 \pm 416 (13) N.S.
territories defended by two males	5276 \pm 797 (14)	6614 \pm 674 (17) N.S.
(b)	Feeder	Control
Females ($n = 10$)	2841 \pm 697	7249 \pm 1149*
Males ($n = 7$)		
territory defended by two males	5473 \pm 741	7933 \pm 1417 N.S.

* $P < 0.01$.

females kept to almost exactly the same areas of the garden in both years and so matched comparisons could be done of the same bird on the same territory either with or without a feeder. These matched comparisons (Table 3b) showed the same result; the presence of feeders resulted in a decrease in female range size (nine of the ten females had smaller ranges in the year they had a feeder) but had no significant effect on male range size.

The influence of the provisioned food on the mating system

In all cases of monogamy and polyandry, all the birds involved within a particular mating combination had access to a feeder when one was present. This was not always true for polygynandrous mating combinations. The eight cases associated with feeders all involved two males sharing two, three or four females. In all cases, the two males had completely overlapping ranges (as, for example, in Fig. 1d) and both used the feeder. However, because the females had exclusive ranges within the males' territory, not all of them necessarily had access to the feeder. In some cases the feeder was located within the range of one of the females and she then had access to the food while the other female(s) involved in the mating combination did not. In other cases, the feeder was on the boundaries of two or more females' ranges and then several females used the food. Whenever two females met at a feeder there were always chases and one ended up displacing the other, so only one used the feeder at any one time. The males often intervened during these disputes, hopping in between the females and keeping them apart. This gave the impression that although the dominant female wanted to chase the subordinate female off, the males wanted her to remain (see discussion).

Even if only one of a male's females had access to the feeder, her smaller range is nevertheless predicted to influence the ease with which he can monopolize her and other females within his territory. We have therefore divided the mating combinations into 'experimental' territories where the male, or males, have access to the feeder and the female, or at least one of the females if there are more than one, have access, and 'control' territories where none of the birds within a mating combination have use of a feeder. As predicted, the effect of the feeder was to change the mating system towards those where males had increased monopolization of females (Table 4). Comparing males who were unpaired plus males who shared one female (polyandry) versus males who had access to one (monogamy) or more females (polygynandry), the difference between experimental and control territories is significant (Table 4; totals column, $\chi^2 = 6.29$, d.f. = 1, $P < 0.02$). An alternative way to analyse the data is to rank the territories in order of male mating success (ratio of females to males); in both 1982 and 1983 the males on feeder territories had significantly greater mating success than controls (Table 4; Mann-Whitney *U*-test, two-tailed, $P < 0.05$).

A possible confounding factor in the interpretation of Table 4 is differences in bird 'quality' between feeder and control territories. It could be argued, for example, that the 'best' females always settled where the feeders were located and these females were then likely to attract the 'best' males, namely those able to monopolize them most effectively. If this were true, then the mating system differences between feeder and control territories could have arisen due to differences in bird quality. This interpretation is unlikely because both males and females were sedentary and tended to occupy the same territories in different years; they did not move to follow the feeders. Matched comparisons can be done for the ten females that were present in both years but had extra food in only one of the years (the ten females in Table 3b). Figure 6 shows that their changes in range were correlated with changes in their mating system. Females whose range increased from 1

TABLE 4. Mating combinations on control and experimental territories (feeder provided) in 1982 and 1983

Mating combination	1982		1983		% Total	
	Feeder	Control	Feeder	Control	Feeder	Control
Unpaired ♂	0	1	0	3	0.0	12.1
Polyandry 3♂♀	0	1	0	1	24.0	48.5
2♂♀	3	9	3	5		
Monogamy ♂♀	7	4	4	6	44.0	30.3
Polygynandry 2♂2♀	0	1	5	1	32.0	9.1
2♂3♀	1	0	1	0		
2♂4♀	0	0	1	0		
3♂2♀	0	1	0	0		
					<i>n</i> = 25	33

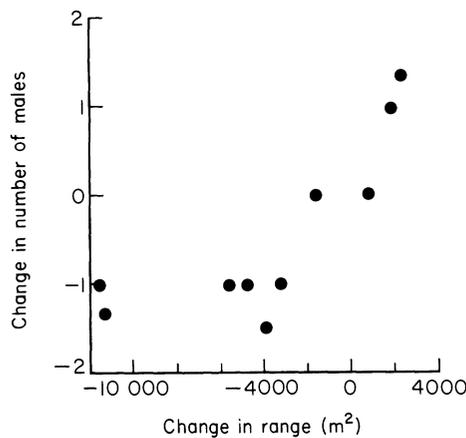


FIG. 6. For the ten females that were present in both 1982 and 1983, but had a feeder in only one of these years, their change in range from 1982 to 1983 was correlated with their change in mating system from 1982 to 1983. A female had more males associated with her when her range increased and fewer males when her range decreased. Spearman rank correlation = 0.790, $P < 0.01$. Changes from ♂♀ to 2♂♀ are scored as a change in one male, from 2♂♀ to 2♂3♀ as a change from 2 to 0.67 males (i.e. a change of 1.33 males) and from 2♂♀ to 2♂4♀ as a change from 2 to 0.5 males (i.e. a change of 1.5 males).

year to the next had more males associated with them while females whose range decreased had fewer males. Thus range size changes bring about mating system changes even considering the same females in different years.

Now considering matched comparisons for the same males on the same territories, who had food in only one of the experimental years. Figure 7 shows that in all cases male mating success was as great or greater in the year with extra food. The analysis can be extended to include territories where there was food provided in only 1 year but different males were present in the 2 years (Fig. 7). Again, mating success was greater in the year the territory had extra food. Furthermore, Fig. 7 shows that when the territories are ranked in order of male mating success, there is a significant correlation between mating success in the year without food and the year with food. This means that the addition of a feeder to a low mating status territory did not increase the mating success of the males to as high a level as the addition of food to a high mating status territory. The effect of a feeder, therefore, appears to add on to natural differences in territory quality already present.

Dunnock mating systems

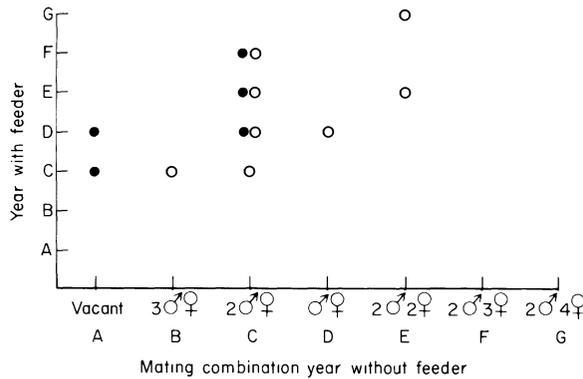


FIG. 7. Matched comparisons for the thirteen male territories that had a feeder in one of the experimental years (1982, 1983) but not the other. The mating combinations are ranked in increasing order of male mating success. (○), The same male(s) were involved in both years or at least one of the males was the same; (●), territories where the male(s) were different in the 2 years. All thirteen territories had as great, or greater, male mating success in the feeder year. Spearman rank correlation = 0.577, $P < 0.05$. See text for discussion.

Finally, we can ask whether the change in mating system brought about by the feeders is due simply to a decrease in female range size and hence their ease of monopolization by males or whether it is also due to changes in male behaviour. Males with feeders do not have larger territories (Table 3) but they may have more spare time in which to attract and defend females. Table 5 compares the time budgets of males with and without feeders during the period 20 February–28 March 1983. Male time budgets taken at this time are likely to be most relevant to determining the mating system because this is the period during which most females settle on their breeding territories. Males with feeders began to sing earlier in the year, sang more, spent less time feeding, and more time perched and interacting with other dunnocks than control males (Table 5). There was, however, no significant variation in male time budget with mating system within either the feeder males or control males (Kruskal-Wallis one way analysis of variance considering time budgets of unpaired, polyandrous, monogamous and polygynandrous males within the feeder males and non-feeder males; no significant differences). For example, within both the feeder and control territories males who sang more or perched more were not more likely to belong to

TABLE 5. Comparison of male time budgets in early spring 1983, for males with feeders and males without. Figures are means, with significant differences tested using Mann-Whitney U -test, 2-tailed

Time budget	Feeder males ($n = 15$)	Control males ($n = 19$)
% time feeding	32.9	72.6*
% time perched	47.8	17.5*
% time preening	3.2	2.9 N.S.
% time interactions	16.1	7.0**
Songs per hour	126.4	56.7*
Interactions per hour	8.6	2.8*
Mean date of first song, (median) (1 = 17 January)	10.4 (5)	28.5 (32)*

* $P < 0.002$, ** $P < 0.02$.

one mating category rather than another. Because male time budget does not vary with mating system, the most likely explanation for the changes brought about by the feeders is that they are due primarily to changes in female range size.

DISCUSSION

We conclude that food distribution influences the range size of a female and this then determines the ease with which she is monopolized by males. Where food patches are dense, female ranges are small, they are easily monopolized and the mating combinations reflect high male mating success (polygyny and polygynandry). Where food patches are sparse, female ranges are large and they are then less easily monopolized giving rise to lower male mating success (polyandry).

In principle, these ideas should also apply to other birds so we are now left with the problem of why the dunnock is apparently unique, at least among British passerines, in having such a variable mating system. Most passerines are monogamous with occasional polygyny, though some are regularly polygynous (Lack 1968). The main unusual feature of the dunnock is the difficulty a male has in maintaining exclusive access to a female. Polyandry is common, and even when a male enjoys access to several females he rarely has exclusive access (polygyny) and usually shares them with another male (polygynandry; see Table 1). Female dunnocks do not have particularly large ranges for small passerines and so their difficulty of monopolization cannot be related to the need of a male to defend an unusually large territory. For example, female robins (which are usually monogamous) on the same study area had a mean range of 5700 m² (range 2550–8300 m², $n = 34$) (Harper 1984) which is not significantly different from that of the female dunnocks. Birkhead (1981) suggested that it is the male-biased sex ratio that gives rise to the high degree of polyandry in dunnocks but this cannot be the main factor because many passerines characterized by a monogamous mating system also have equally male-biased sex ratios (e.g. for robins on the study area, the sex ratios at the start of the breeding seasons in 1981, 1982 and 1983 were respectively 27 ♂ 23 ♀, 27 ♂ 21 ♀, 29 ♂ 21 ♀, Harper 1984). In most passerines these 'extra' males remain unpaired; the oddity in the dunnock is that most end up in polyandrous associations either by territory coalescence or by forcing themselves onto pair territories to form trios.

We agree with Snow & Snow (1982) that the difficulty males have in maintaining an exclusive territory is linked to the dunnock's foraging specialization on small prey in dense cover. Although males can easily spot intruders who sing, and so can set up exclusive song territories (see results), they cannot easily spot intruders who trespass to forage because they usually remain hidden in the dense undergrowth. Likewise, any persistent intruder who accepted subordinate status as a beta male, and attempted to mate with the female, would also be difficult to drive away because he could hide on the territory for long periods. This is almost certainly why the alpha male guards his female so closely during the egg laying period, remaining within 5 m of her throughout and chasing off other males who approach her (Davies 1985). It would be more or less impossible for him to protect his paternity by attempting to maintain an exclusive territory. Despite the close guarding, however, the incentive for a beta male to remain on the territory is high because alpha males often lose their females in the dense undergrowth. If a beta male is then the first to find her, he can mate with her undetected. When an alpha male loses his females, he searches frantically all over the territory but even so it is often 10 min (once 3 h) before he manages to find her again.

There is another factor, however, which is important in giving rise to the complex mating system, namely a conflict of interest between males and females over the mating combination that maximizes an individual's reproductive success. Females not only accept copulations from beta males, they actively encourage them by attempting to escape the guarding of the alpha male. For example, they often fly off suddenly low through the vegetation, changing direction as if to shake him off. If the female escapes his attentions, she may then approach the beta male and actively solicit matings from him. The advantage to her of doing this is that the beta male will only feed her chicks if he has copulated with her (Davies 1983). Nestlings fed by both an alpha and a beta male get more food, fledge at a heavier weight and survive better than chicks fed by just one male. Therefore females can increase their reproductive success by getting the beta male to copulate. From the alpha male's point of view, however, the increased success of a trio-fed brood does not compensate him for his loss of paternity and so it pays him to prevent the beta male from mating and to drive him off if at all possible (Davies 1985).

The increased nestling weight in a trio-fed brood is probably also linked ultimately to the dunnock's foraging specialization on small prey. The chicks are fed on small insects which are very time consuming to collect and it seems likely that the rate at which food is delivered to the nest is limited not primarily by food abundance but rather by the work force available to collect it. It may therefore pay the female dunnock, more so than a passerine that exploits easily collected bonanzas of large prey (e.g. caterpillars), to have more than one male to help care for the chicks (Houston & Davies 1985).

It is interesting to consider whether a female could increase the chances that her brood will be fed by two males rather than one, by the tactic of increasing her range to a size where one male found it impossible to monopolize her. This hypothesis would predict that female ranges should be larger than expected from foraging requirements alone. The results of the feeder experiment, at least, provide no evidence that females behave like this. They were apparently happy to contract their ranges in the presence of extra food, even though this resulted in them having a mating combination that made it less likely that two males would be available to feed the chicks (more monogamy and less polyandry on feeder territories—Table 4). Although there were more cases of polygynandry on feeder territories, here a female had to share the males' parental investment with other females and her chicks did not achieve as high weights as cases of polyandry where she had the undivided help of two males.

Although females can enjoy high reproductive success with polyandry if they do manage to copulate with both the beta and alpha male, they can sometimes suffer from the continuous harassment by two males during the egg laying period. The prolonged chases by two males may interfere with female foraging and reproductive activities and furthermore, if the beta male does not mate he sometimes interferes with the reproductive attempt by destroying eggs and perhaps chicks. Overall, including both cases where alpha and beta males mate and cases where only the alpha male mates, the reproductive success of females in polyandrous associations is not higher than for monogamy. Therefore there is no incentive for a female to increase her range to gain another male unless she can be certain of getting both males to copulate (Davies 1985).

In summary, the difficulty a male has in maintaining an exclusive territory and the existence of sexual conflict over the acceptance of a beta male are both probably linked ultimately to a feeding ecology involving exploitation of small prey in dense undergrowth. Any male bias in the sex ratio will, of course, increase the competition for females and the level of polyandry. Reproductive success in the various mating combinations will be

discussed in another paper. Our main point here is that sexual conflict is played on an ecological stage with foraging ecology and female range size lying at the heart of a male's ability to monopolize mates.

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REFERENCES

- Arak, A. (1983). *Male-male competition and mate choice in frogs and toads*. Ph.D. thesis, Cambridge University.
- Birkhead, M. E. (1981). The social behaviour of the dunnoek, *Prunella modularis*. *Ibis*, **123**, 75–84.
- Clutton-Brock, T. H. & Harvey, P. H. (1977). Primate ecology and social organisation. *Journal of Zoology*, **183**, 1–39.
- Crook, J. H. (1964). The evolution of social organization and visual communication in the weaver birds, Ploceinae. *Behaviour Supplement*, **10**, 1–178.
- Darwin, C. (1871). *The Descent of Man and Selection in Relation to Sex*. John Murray, London.
- Davies, N. B. (1983). Polyandry, cloaca-pecking and sperm competition in dunnocks. *Nature*, **302**, 334–336.
- Davies, N. B. (1985). Cooperation and conflict among dunnocks, *Prunella modularis* in a variable mating system. *Animal Behaviour*, **33**, (in press).
- Davies, N. B. & Lundberg, A. (1985). The influence of food on time budgets and the timing of breeding in dunnocks. *Prunella modularis*. *Ibis*, (in press).
- Emlen, S. T. & Oring, L. W. (1977). Ecology, sexual selection, and the evolution of mating systems. *Science*, **197**, 215–223.
- Ewald, P. W. & Rohwer, S. (1982). Effects of supplemental feeding on timing of breeding, clutch size and polygamy in red winged blackbirds, *Agelaius phoeniceus*. *Journal of Animal Ecology*, **51**, 429–450.
- Harper, D. G. C. (1984). *Economics of foraging and territoriality in the European robin* *Erithacus rubecula*. Ph.D. thesis, Cambridge University.
- Houston, A. I. & Davies, N. B. (1985). Evolution of cooperation and life history in dunnocks. *Behavioural Ecology: The Ecological Consequences of Adaptive Behaviour* (Ed. by R. Sibly & R. H. Smith). British Ecological Society Symposium. Blackwell, Oxford. (in press).
- Jarman, P. J. (1974). The social organisation of antelope in relation to their ecology. *Behaviour*, **48**, 215–267.
- Karanja, W. K. (1982). *The biology of the dunnoek, Prunella modularis, with special emphasis on its breeding biology*. D. Phil. Thesis, Oxford University.
- Lack, D. (1968). *Ecological adaptations for breeding in birds*. Methuen, London.
- Odum, E. P. & Kuenzler, E. J. (1955). Measurement of territory and home range size in birds. *Auk*, **72**, 128–137.
- Pleszczyńska, W. K. (1978). Microgeographic prediction of polygyny in the lark bunting. *Science*, **201**, 935–937.
- Pleszczyńska, W. K. & Hansell, R. I. C. (1980). Polygyny and decision theory: testing of a model in lark buntings, *Calamospiza melanocorys*. *American Naturalist*, **116**, 821–830.
- Smith, J. N. M., Yom-Tov, Y. & Moses, R. (1982). Polygyny, male parental care and sex ratios in song sparrows: an experimental study. *Auk*, **99**, 555–564.
- Snow, B. & Snow, D. (1982). Territory and social organization in a population of dunnocks, *Prunella modularis*. *Journal of the Yamashina Institute for Ornithology*, **14**, 281–292.
- Svensson, L. (1970). *Identification Guide to European Passerines*. Naturhistoriska Riksmuseet, Stockholm.
- Trivers, R. L. (1972). Parental investment and sexual selection. *Sexual Selection and the Descent of Man* (Ed. by B. Campbell), pp. 139–179. Aldine, Chicago.
- Verner, J. (1964). Evolution of polygamy in the long-billed marsh wren. *Evolution*, **18**, 252–261.
- Verner, J. & Willson, M. F. (1966). The influence of habitats on mating systems of North American passerine birds. *Ecology*, **47**, 143–147.

- Wells, K. D. (1977).** The social behaviour of anuran amphibians. *Animal Behaviour*, **25**, 666–693.
- Wittenberger, J. F. (1980).** Food supply, vegetation structure and polygyny in bobolinks, *Dolichonyx oryzivores*. *Ecology*, **61**, 140–150.
- Wrangham, R. W. (1980).** An ecological model of female-bonded primate groups. *Behaviour*, **75**, 262–300.

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