Behav Ecol Sociobiol (1993) 32:259–263

Behavioral Ecology and Sociobiology

Ontogeny of dispersal distances in young Spanish imperial eagles

M. Ferrer

Estación Biológica de Doñana CISC, Avd. Maria Luisa, Pabellón de Perú, E-41013 Sevilla, Spain

Received March 25, 1992 / Accepted September 21, 1992

Summary. I studied factors influencing dispersal distances in 30 young Spanish imperial eagles (*Aquila adalberti*) radio-tagged in southwestern Spain in 1986–1990. The mean dispersal distance between the natal nest and the settling area was 138 km. Every young bird reached its maximum dispersal distance within 4 months of its departure from the natal population. No significant differences between the sexes were detected in maximum dispersal distance, but females spent more time in the more distant settling areas. Dispersal distance was not related to the date of departure from the natal population. Dispersal distance was significantly longer for birds that hatched earlier and that had lower blood urea levels, indicating that better-nourished young had longer displacements. These results are not in accordance with the competitive displacement hypothesis.

Introduction

Dispersal influences gene flow between populations, as well as the colonization process. The flow of genes influences the geographical variation of natural populations and, in effect, the evolution of diversity (Moore and Dolbeer 1989). Nevertheless, the ultimate mechanisms of dispersal in vertebrates are the object of discussion (Johnson and Gaines 1990). Almost all the information published about avian dispersal is based on studies of ring recoveries or occasional observations of individuals with wing tags (Johnson and Gaines 1990). Avian dispersal studies based on continuous following of radio-tagged specimens over a long period are scarce.

In virtually every dispersal study of birds a leptokurtic distribution has been found (Buechner 1987; Miller and Carroll 1989; Rodgers and Klenner 1990). It has been suggested that such a distribution could be generated by competition during territory acquisition. Those individuals that are displaced longer distances, forming the tail of the distribution, are the individuals at lower competitive advantage, which would probably be the last to hatch and disperse (Murray 1967; Waser 1985). There are several alternative explanations for polymorphism of dispersal distances. They may be genetically based; for some species, heritability has been estimated from the similarity of displacements between siblings (Greenwood et al. 1979; Newton and Marquiss 1983; but see Noordwijk 1984). Many authors have described sex differences in dispersal distances (Moore and Ali 1984). In birds, females tend to be the dispersing sex (Dhondt 1979; Greenwood et al. 1979; Greenwood 1980; Newton and Marquiss 1983; Korpimäki et al. 1987; Drilling and Thompson 1988). Such behaviour has been interpreted as a mechanism to decrease inbreeding (Greenwood et al. 1979; Greenwood 1980).

Young Spanish imperial eagles *Aquila adalberti* leave their natal population on average at the age of 137 days, and the average age at first settlement was 164 days (Ferrer 1990a). Young Spanish imperial eagles use different temporary settling areas. Each area was used intensively for a variable but short period, and each individual used the same areas (between three and eight) in rotation during at least the first 3 years of life, returning occasionally to the natal population (Ferrer in press).

The aim of this paper is to examine whether the competitive displacement hypothesis could explain the distribution of dispersal distances observed in a Spanish imperial eagle population. I test whether the individuals with longer displacements towards the more distant settling areas are later to hatch and subjected to worse conditions during their development, as predicted by the hypothesis of competitive displacement.

Material and methods

The study was carried out in the Spanish imperial eagle population of Doñana National Park, southwest Spain, from 1986 to 1990. This population consisted of 15 breeding pairs at a high density and has remained stable for at least the last 18 years (Ferrer and Calderón 1990). The Spanish imperial eagle population at Doñana is apparently isolated from other breeding populations of the same species, the nearest of which is 300 km away. The Spanish imperial eagle is a large bird of prey (2500–3500 g, Ferrer 1990a), with a low reproductive rate and an immaturity period of 4–5 years (Ferrer and Calderón 1990).

To carry out the study, 30 young eagles were equipped with solar radiotransmitters (type HSPB 1400 3XA, Wildlife Materials Inc.) during the years 1986–1988 inclusive. Transmitters were fixed on the back of the nestlings by a harness (Kenward 1987), at the end of the nestling period (50–70 days of life). The weight of transmitter and harness ranged between 28 g and 37 g (approximately 1% of the bird's weight). During 1989 and 1990 only the survivors from previous years were observed. Hatching dates were accurately known from previous checks during reproduction. The sex was determined according to the forearm length (Ferrer and De le Court 1992). Of the 30 nestlings, 14 were males and 16 females, and 8 of them were marked in 1986, 8 in 1987 and 14 in 1988. In total, 5 chicks from broods of one young, 14 from broods of two and 11 from broods of three were studied.

To determine nutritional condition, I measured blood urea levels. As is known for many bird species, including Spanish imperial eagles, when tissue protein sources are mobilized by starvation, provoking an increase in nitrogenous excretory components in the blood, the urea value increases (Okumura and Taski 1969; Jeffrey et al. 1985; Ferrer et al. 1987; Garcia-Rodriguez et al. 1987a; Ferrer 1990a, b). A 2-ml blood sample was extracted from the radial vein of the wing at the end of the nestling period, when the nestlings were between 50 and 70 days old. Blood samples were collected in lithium-heparin tubes. Blood was centrifuged and plasma separated (10 min at 3000 rpm) no more than 6 h after the sample was drawn. Blood analyses were carried out in a computer process-controlled autoanalyser (Hitachi 705 multichannel autoanalyser, with the reagents recommended by Boehringer-Mannheim Inc.). All blood samples were extracted between 1100 and 1500 h to minimise circadian variation in biochemical parameters (Garcia-Rodriguez et al. 1987b; Ferrer 1990b).

Three teams were used to track the young. One was located in a 35-m tower in the middle of the natal population, and recorded the flight direction of every young bird every half hour for the first 2 months of dispersal and at least once a day during the remainder of the study. The second team carried out searches, by light aircraft, of all individuals within a circle of 300 km radius, centred on the natal population. Two flights a week were made during September, October and November, and 2-monthly flights during the rest of the year, totalling 256 flying hours. Initial searches used a non-directional antenna, usually fixed below the aircraft. When individuals were detected, their position was determined by triangulation with a directional antenna and the compass of the aircraft. The third team made observations from a vehicle, equipped with a non-directional antenna with a magnetic base fixed to the roof; triangulation was done using a directional antenna when a radio-tagged eagle was detected.

During the study, the three teams sought at least two contacts a week for each individual bird. A total of 2106 contacts with 30 radio-tagged young outside the natal population were obtained. I consider as the first departure the first time that a young bird moved away from the natal population, leaving the Doñana area, and when the site of contact was more than 20 km from the natal nest. Dispersal distance was defined as the distance between the natal nest and the settling area.

In the analysis of the distribution of dispersal distances, two distance measures were used: (1) the maximum distance recorded for each individual during the entire dispersal period studied (D_{max}), and (2) the maximum distance at which each individual was located within 20 days of its first departure from the natal population (D_{age}). In every case, the distance between the young bird's location and its natal nest was measured on a 1:50000 map.

Results

Of the 30 young equipped with radio-transmitters 26 survived the dependence period and started dispersal. Of these 26 I immediately lost contact with 2. Of the 24 that were followed, 2 showed unusually great displacements (330 and 430 km). The other 22 were divided over two dispersal areas near the National Park of Doñana; 13 used the area of Cádiz and 9 the area of Huelva (these areas are less than 150 km from Doñana National Park, Fig. 1). Assuming that the young with which I lost contact were displaced to other areas, 84.4% of the dispersing young used one of the two areas near the natal population throughout their immature life (to the present). Within these two dispersal areas, each young used between three and eight settling areas (Ferrer in press). Returns to the natal area occurred throughout the dispersal period studied. There were no significant differences between sexes in the frequency of returns ($F=0.148$, $df=12$, $P=0.711$) or in their duration ($F=0.035$, $df=54$, $P=0.854$).

The mean of the maximum distance of dispersal (D_{max}) was 138 km (range 50–450, $n=24$). Expressed as number of territories potentially crossed (radius of the area occupied by a pair = 3.25 km; González 1989), the average was 21.25 territories. D_{age} did not increase significantly with age ($F=0.349$, $df=67$, $P=0.9752$). All young reached their maximum dispersal distance within 4 months of their departure from the natal population. At this age, dispersal distances showed a leptokurtic distribution (Fig. 2). No differences in D_{max} according to brood size were detected (Table 1). Between sexes, no significant differences were detected in D_{max} (Table 1), but females were located more frequently in the more distant temporary settling areas (D_{age}, $F=9.997$, $df=1,66$, $P=0.0024$). No significant differences were found between years in D_{max} (Table 1). D_{max} was not related to the age at which the young left the nest ($r=-0.030$, $df=16$, $P=0.917$), the age of the independence of the young ($r=0.2613$, $df=16$, $P=0.328$), or the date of de-

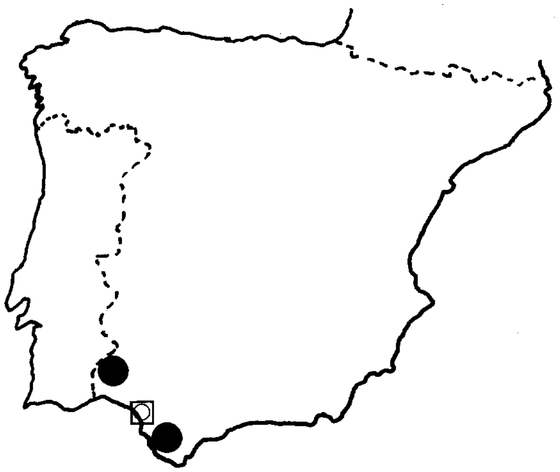

Fig. 1. Dispersal areas used by the dispersing immature Spanish imperial eagles (*black circles*) and the natal population of Doñana National Park (*circle in square*)

Table 1. Effects of different factors on the maximum dispersal distance (D_{max} in km) of young Spanish imperial eagles

	Average	*n*	*F*	*df*	*P*
Brood size					
1	95.0	5			
2	153.8	8	0.489	2.18	0.621
3	132.5	8			
Sex					
Male	123.6	11			
Female	140.6	10	0.139	1.19	0.717
Year					
1986	97.7	6			
1987	137.5	5	0.256	2.18	0.777
1988	140.3	11			
Nest					
1	91.2	2			
2	386.7	2			
3	140.0	2			
4	219.5	2	9.015	6.7	0.005
5	105.5	2			
6	59.3	2			
7	56.8	2			

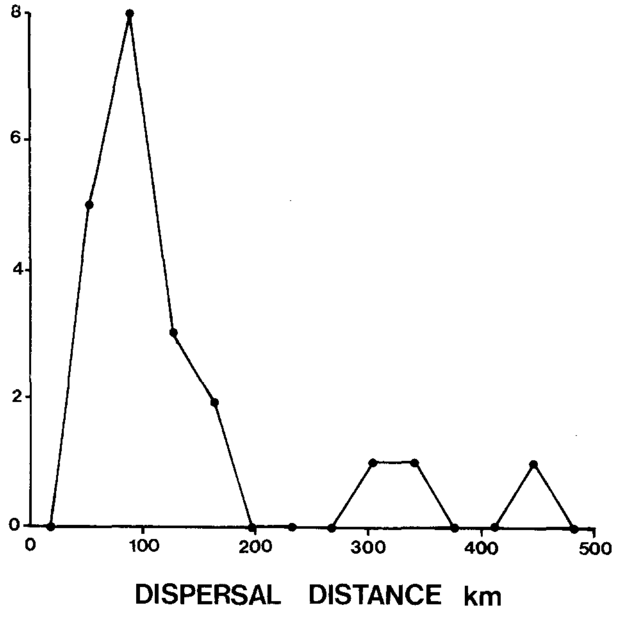

Fig. 2. Distribution of dispersal distances (D_{max}) in the Spanish imperial eagle

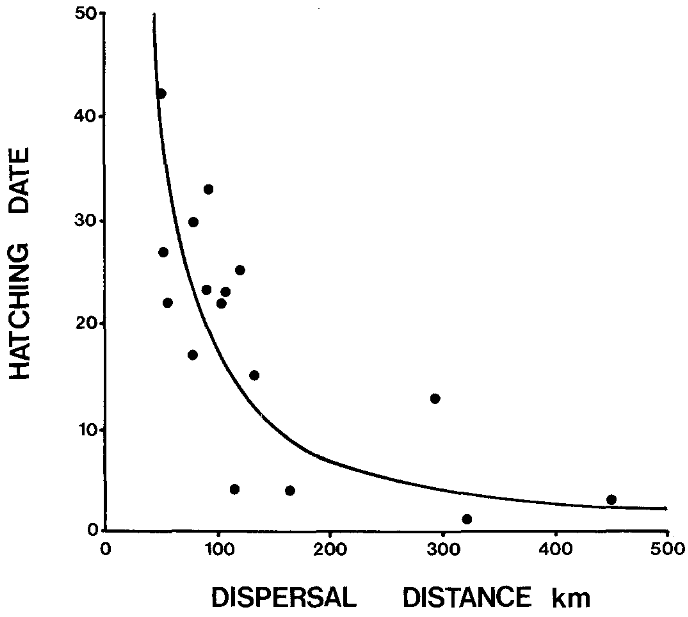

Fig. 3. Relation between the maximum distance (D_{max}) of dispersal and the hatching date, considering as data 1 the earliest hatching recorded during the 3 years of the study, $r = -0.771$, $P = 0.0001$

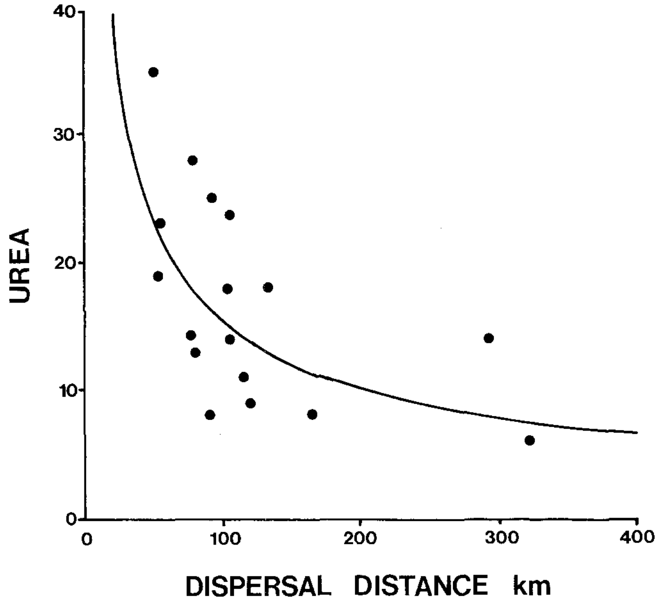

Fig. 4. Relation between the urea level in blood, measured at the end of the stay in the nest, and the maximum distance (D_{max}) of dispersal, $r = -0,629$, $P = 0.0067$

parture from the natal population ($r = 0.195$, $df = 13$, $P = 0.715$).

A very significant relationship was found between D_{max} and the relative hatching date (considering the earliest hatching recorded in the 3 years as day 1): birds hatched earlier dispersed farther (multiplicative regression $r = -0.771$, $F = 23.527$, $df = 1,16$, $P = 0.0001$, Fig. 3). Birds with lower blood urea levels also dispersed farther (multiplicative regression $r = -0.629$, $F = 9.906$, $df = 1,15$, $P = 0.0067$, Fig. 4). Siblings of the same brood tended to move similar distances (Table 1). However, when the residuals of the regression of urea level against D_{max} were used, the family effect disappeared ($F = 0.836$, $df = 12$, $P = 0.583$).

Discussion

The juvenile displacements recorded in the Spanish imperial eagle population from Doñana, are longer, in terms of territories potentially crossed, than the ones found in the natal dispersal of *Otus asio* (Belthoff and Ritchison 1989), *Parus major* (Greenwood et al. 1979), *Zonotrichia leucophrys* (Baker and Newaldt 1978), *Sitta europea* (Matthysen and Schmidt 1987), *Parus atricapilla* (Weise and Meyer 1979), but smaller than the ones recorded in *Accipiter nisus* (Newton and Marquiss 1983). This parameter, in any case, is influenced by many factors, such as the distribution and patchiness of the potential habitat available for young, and can vary greatly among populations of the same species (Belthoff and Ritchinson 1989). The typical leptokurtic distribution of distances is generated at the beginning of the dispersal phase. On the other hand, in this study, I have only recorded juvenile displacements during the first 3 years of immaturity, so I cannot dismiss the possibility that distances decrease at the time of first reproduction. In any case, no variation of the dispersal distance with age was observed in my data, which shows that, at least during the first 3 years of immaturity, this behaviour was maintained.

The distribution of dispersal distances found during these first years of immaturity in the Spanish imperial eagle is very similar to that described for the natal dispersal of other species of birds (Dhondt 1979; Greenwood et al. 1979; Greenwood 1980; Newton and Marquiss 1983; Korpimäki et al. 1987; Drilling and Thompson 1988). The current hypothesis to explain the generation of this kind of distribution suggests that the long-distance dispersers would be removed by competition, and that the territories near the natal population are occupied by earlier and more competitive dispersers (Murray 1967; Waser 1985). According to this hypothesis, a direct relationship between the date of departure from the natal population (or the hatching date) and the dispersal distance would be expected, since the dispersal distance for later dispersers is longer. However, in spite of many studies involving different species this has not yet been confirmed [e.g. *Passer domesticus* Lowther 1979), *Accipiter gentilis* (Newton and Marquiss 1983), *Parus major* (Dhondt 1979; Greenwood et al. 1979), *Sitta europaea* (Matthysen and Schmidt 1987), *Aegolius funereus* (Korpimäki and Lagerström 1988) and *Otus asio* (Belthoff and Ritchison 1989)].

The results of this study show that there is no relationship between the dispersal distance and the date of departure from the natal population. Nevertheless, there is a strong relationship between hatching date and dispersal distance, but it is exactly opposite to the expected one, with the earlier young dispersing over longer distances. Also, the relationship with urea level shows that it is the young in better physical condition and whose growth has been better that move the longest distances from the natal population. Therefore, the hypothesis of competitive displacement of the long-distance dispersers seems unlikely to apply in this case.

An alternative hypothesis for polymorphism in dispersal behaviour is that the dispersal distance is genetically fixed (Waser 1985). Some authors have suggested a certain degree of heritability of dispersal distances, based on the similarity of the distances covered by siblings, proposing that the long-distance dispersers would inherit this feature (Dhondt 1979; Newton and Marquiss 1983). In the Spanish imperial eagle, similarities in dispersal distance of siblings from the same brood are more likely to be due to covariance of other environmental factors affecting the nests than to be genetically determined. In fact, the significance of sibling effects disappeared when the effect of urea level was discounted. Since the level of urea is very similar within a brood and very different between nests (Ferrer 1990a), and the same happens with the hatching date, we would expect young from the same nest to show displacements of the same length, as described by other authors for different species (Dhondt 1979; Newton and Marquiss 1979; Weise and Meyer 1979). Two nestlings from other populations of the species more than 300 km away (from Doñana), introduced at a few days of age into nests of the Doñana population also containing the original nestlings, had dispersal displacements similar to those of their adoptive siblings.

Differences between sexes in dispersal distances have been interpreted as a way of decreasing inbreeding (Greenwood et al. 1979; Greenwood 1980). In the Spanish imperial eagle, females spent more time in the more distant areas, but they returned to the natal population occasionally during all their immature life, as did the males. The frequency and length of the returns was the same for both sexes. Hence this type of sex-biased dispersal does not seem to occur.

In conclusion, only the existence of an important selective advantage in the dispersal process could explain the behaviour detected in the Spanish imperial eagles of the Doñana population, since the individuals which moved longer, distances were the earliest to hatch and the best nourished, and probably had the greatest competitive advantage. The ability to carry out long-distance displacements would be found in nestlings in better physical condition. This would be determined by an optimum level of nutrients during the development of the chick. This would also explain the relation between dispersal distances and both the urea level and the hatching date, which are intimately related, with lower urea values in young that hatch earlier (Ferrer 1990a). If the suitability of settling areas for the Spanish imperial eagle is highly variable, and there is no particular cost in searching for optimal sites, we could reject the competition model where less competitive individuals disperse further, and propose instead an alternative competition model in which superior competitors would gain by moving farther.

Acknowledgements. I am indebted to L. Garcia, R. Cadenas and J.J. Negro for helping in the field. I thank F. Hiraldo, J.A. Donazar, J.J. Negro, P. Waser and F.S. Dobson for suggestions on the manuscript. This study was supported by DGICYT, project number PB87-0405 and by a postdoctoral grant from Consejo Superior de Investigaciones Cientificas.

References

Baker MC, Newaldt LR (1978) Song dialects as barriers to dispersal in white-crowned sparrows, *Zonotrichia leucophrys*. Evolution 32:712–722

Belthoff JR, Ritchison G (1989) Natal dispersal of eastern screech-owls. Condor 91:254–265

Buechner M (1987) A geometric model of vertebrate dispersal: tests and implications. Ecology 68:310–318

Dhondt AA (1979) Summer dispersal and survival of juvenile great tits in southern Sweden. Oecologia 42:139–157

Drilling NE, Thompson CF (1988) Natal and breeding dispersal in house wrens (*Troglodytes aedon*). Auk 105:480–491

Ferrer M (1990a) Dispersión juvenil de la población de águilas imperiales del Parque Nacional de Doñana. Ph.D. thesis, Universidad de Sevilla

Ferrer M (1990b) Hematological studies in birds. Condor 92:1085–1086

Ferrer M (in press) Reduction in hunting success and settlement strategies in young Spanish imperial eagles. Anim Behav

Ferrer M, Calderón J (1990) The Spanish imperial eagle *Aquila adalberti* in Doñana National Park: a study of population dynamics. Biol Conserv 51:151–161

Ferrer M, De le Court C (1992) Sex determination in the Spanish imperial eagle. J Field Ornithol 62:359–364

Ferrer M, Garcia-Rodriguez T, Carrillo JC, Castroviejo J (1987) Hematocrit and blood chemistry values in captive raptors. Comp Biochem Physiol 87A:1123–1127

Garcia-Rodriguez T, Ferrer M, Carrillo JC, Castroviejo J (1987a) Metabolic responses of *Buteo buteo* to long-term fasting and refeeding. Comp Biochem Physiol 87A:381–386

Garcia-Rodriguez T, Ferrer M, Recio F, Castroviejo J (1987b) Circadian rhythms of determined blood chemistry values in buzzards and eagle owls. Comp Biochem Physiol 88A:663–669

Gonzalez LM (1989) Historia natural del águila imperial ibérica. Ph.D. thesis, Universidad Autonoma de Madrid

Greenwood PJ (1980) Mating systems, philopatry and dispersal in birds and mammals. Anim Behav 28:1140–1162

Greenwood PJ, Harvey PH, Perrins C (1979) The role of dispersal in the great tit (*Parus major*): the causes, consequences and heritability of natal dispersal. J Anim Ecol 48:123–142

Jeffrey DA, Peakall DB, Miller DS, Herzberg GR (1985) Blood chemistry changes in food-deprived herring gulls. Comp Biochem Physiol 81A:911–913

Johnson ML, Gaines MS (1990) Evolution of dispersal: theoretical models and empirical tests using birds and mammals. Annu Rev Ecol Syst 21:449–480

Kenward RE (1987) Wildlife radio tagging. Academic Press, London

Korpimäki E, Lagerström M (1988) Survival and natal dispersal of fledglings of Tengmalm's owl in relation to fluctuating food conditions and hatching date. J Anim Ecol 57:433–441

Korpimäki E, Lagerström M, Saurola P (1987) Field evidence for nomadism in Tengmalm's owl *Aegolius funereus*. Ornis Scand 18:1–4

Lowther PE (1979) Growth and dispersal of nestling house sparrows: sexual differences. Bird Band 51:23–29

Matthysen E, Schmidt K (1987) Natal dispersal in the nuthacht. Ornis Scand 18:313–316

Miller GL, Carroll BW (1989) Modelling vertebrate dispersal distances: alternatives to geometric distribution. Ecology 70:977–986

Moore J, Ali R (1984) Are dispersal and inbreeding avoidance related? Anim Behav 32:94–112

Moore WS, Dolbeer RA (1989) The use of banding recovery data to estimate dispersal rates and gene flow in avian species: case studies in the red-winged blackbird and common grackle. Condor 91:242–253

Murray BG (1967) Dispersal in vertebrates. Ecology 48:975–978

Newton I, Marquiss M (1983) Dispersal of sparrowhawks between birthplace and breeding place. J Anim Ecol 52:463–477

Noordwijk AJ van (1984) Problems in the analysis of dispersal and a critique on its 'heritability' in the great tit. J Anim Ecol 53:533–544

Okumura J, Taski I (1969) Effect of fasting, refeeding and dietary protein levels on uric acid and ammonia content of blood, liver and kidney in chickens. J Nutr 97:316–320

Rodgers AR, Klenner WE (1990) Competition and the geometric model of dispersal in vertebrates. Ecology 71:818–822

Waser PM (1985) Does competition drive dispersal? Ecology 66:1171–1175

Weise CM, Meyer JR (1979) Juvenile dispersal and development of site-fidelity in the black-capped chickadee. Auk 96:40–55