Body-Mass Dependent Fledging Order in the Great Tit

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I studied the order of nest-leaving within broods of hole-nesting Great Tits (*Parus major*) and specifically the effect of nestling quality. The study was conducted in Göteborg (southwestern Sweden) in a park composed of a mosaic of deciduous and coniferous trees. I banded nestlings at 15 days of age with unique combinations of colored bands, and measured mass and tarsus length. Close to a forecasted nest-leaving date, the nest was observed from a blind until the nestlings fledged. When the banded nestlings left the nest, their jumping order was observed with binoculars and a telescope and recorded. We monitored seven nests, but one was excluded subsequently because of uncertain identification of the nestlings.

Departure from the nest box.—Nestlings usually left the nest between 0630 and 1200. Of 58 nestlings, 0 left the nest after 1200, which is in accordance with the suggestion that the young need time to examine the surroundings before dark (Perrins 1979). Nestlings that remained in the nest box at 1200 did not leave until the next morning. In a brood, the interval between the times the first and the last nestling left the nest could be >24 h. The shortest interval between the first and the last departure was 10 min.

After they left the box, the fledglings scattered rapidly in all directions until they were ca. 60-80 m apart. Fledglings usually perched 5-10 m above the ground, close to the trunk in trees. The parents located their newly fledged offspring by following their begging calls. When located, the fledgling was fed intensively by both parents until silent. Satiated fledglings remained silent for ca. 20 min. If fledglings and nestlings begged simultaneously, parents favored fledglings. Presumably, predation was reduced by feeding fledglings before nestlings. The second day after fledging, fledglings formed a family party (Perrins 1979).

Fledgling order.—I analyzed the correlation between fledging order and body mass, tarsus length, and an index of body condition (the cube root of body mass is divided by tarsus length) by a Pitman permutation test (Lehman 1958, Bradley 1968) with the nest-box effect removed. All measurements were transformed to produce a brood mean of unity ($x_i/\bar{x}_{\text{brood}}$). Fledging order correlated negatively with body mass and tarsus length. With one exception, larger nestlings tended to jump earlier than lighter individuals. The first nestling was lighter than the next four in the jump order (Fig. 1). I found no significant correlation with body condition (Table 1).

Body-mass differences explained most of fledging order within broods (Table 1; Fig. 1). Size has been proposed as an important determinant of social rank. Presumably the individual's ability to fight is enhanced by a large body size (Wilson 1975; Garnett 1976, 1981; Searcy 1979; Clutton-Brock et al. 1982; Järvi and Bakken 1984; but see also Arcese and Smith 1985). Accordingly larger nestlings within a brood are expected to dominate their nest mates (Gottlander 1987, Forbes and Ankney 1987). If an individual's decision to leave depends on what the other siblings do, the order may reflect a social hierarchy within a brood. Predation risk has to be balanced with food demand (Caraco 1979). Accordingly, if predation risk is low in the nest but high outside, and food availability is adequate, there is no reason to leave the nest. I observed no nest predation in ca. 320 breeding attempts during the past 4 yr (1984-1987); and I observed that predation risk was low in the nest. Mammals, however, can raid nests and usually kill all nestlings (Dunn 1977, Perrins 1979). Outside the nest, fledglings faced a severe predation risk. The Eurasian Sparrowhawk (*Accipiter nisus*) is a major predator (Perrins 1979, Perrins and Geer 1980, Newton 1986), and 2-4 pairs used the study area.

The first nestling to leave may have no clue whether there is a predator outside, but can provide information to its nest mates. In the nest, the dominant individual monopolizes the food brought by the parents (Bengtsson and Rydén 1983, Gottlander 1987, Forbes and Ankney 1987). Pied Flycatcher (*Ficedula hypoleuca*) nestlings appear to struggle for the best begging position in the nest, which is commonly occupied by the largest nestling (Gottlander 1987). This may produce an unstable dominance hierarchy within the brood. As long as each nestling receives a suf-

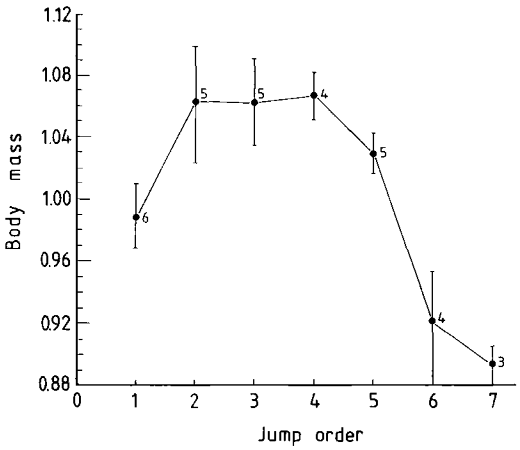

Fig. 1. Jump order in relation to transformed values of body mass (see text). Numbers in graph indicate sample size (n) for each point.

TABLE 1. Joint probability values (P) of correlations between jump order and measurement of body mass, tarsus length and body-condition index. The level of significance was increased by the exclusion of the first jump order. I = all jump orders included; II = first jump order excluded.

Variable	P (I)	P (II)	Slope of correlation
Body mass	0.004	0.0004	negative
Tarsus length	0.03	0.05	negative
Body-condition index	0.3	0.5	—

ficient amount of food, none will leave the nest. However, if the parents are not able to provide adequate food and distribute it equally among nestlings, a starving individual may leave despite a high risk of predation (Kenward 1978; above). By this reasoning, I expected nestlings who jumped first not necessarily to be smallest with respect to body mass but to be in poorer physical condition than those that jumped subsequently. The prediction was supported by a random body mass (ANOVA, $P = 0.6362$) and by the low body-condition index for the first nestling to jump (Table 2). There was, however, a difference of 5-7 days between measurements and observations, which probably affected the body-condition index because stability in mass cannot be assumed (Holcomb 1970).

After one nestling has left, the dominant nestling must also leave the nest to continue access to the food brought by the parents. Subsequently, the remaining nestlings leave, as parents favor fledglings. Conceivably the fledging order reflects the dominance hierarchy within a brood (Fig. 1). The first fledgling to leave may not necessarily be the highest ranked individual, but rather an individual in poor condition. This turns the problem into a decision based on what the other nestlings do (Grafen 1987). Great Tit nestlings of large mass have higher survival probability (Perrins 1965) and the three largest nestlings have the greatest chance to breed eventually (Wallin and Lemel in prep.).

TABLE 2. Untransformed values of mean and standard error for body mass (g), tarsus length (mm), and a body-condition index ($\text{mass}^{1/3}$/tarsus length) at day 15 tabulated for corresponding jump order. Sample size is in parentheses.

Jump order	Mass ± SE	Tarsus ± SE	Condition ± SE
1 (6)	16.5 ± 1.0	22.3 ± 0.3	0.1137 ± 0.0018
2 (5)	17.5 ± 0.9	22.6 ± 0.3	0.1149 ± 0.0016
3 (5)	17.5 ± 0.7	22.5 ± 0.3	0.1151 ± 0.0011
4 (4)	17.2 ± 1.3	22.1 ± 0.4	0.1168 ± 0.0008
5 (5)	15.6 ± 1.3	22.2 ± 0.4	0.1148 ± 0.0018
6 (4)	15.0 ± 1.5	21.2 ± 0.8	0.1158 ± 0.0011
7 (3)	15.5 ± 0.5	21.8 ± 0.1	0.1144 ± 0.0014

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Genetic Structure and Gene Flow in the Northern Bobwhite

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Electrophoretic studies have revealed that birds generally exhibit less interpopulational genetic differentiation than is typical of other vertebrates (Corbin 1977) and that genetic variation is usually partitioned within rather than among populations (Barrowclough 1980). Despite these observations, avian electrophoretic data have not been extensively utilized to estimate levels of gene flow among populations (Rockwell and Barrowclough 1987). Recently Slatkin (1985a, b) and Barton and Slatkin (1986) have shown that the conditional average frequencies of private alleles (alleles unique to a single population) provide a convenient estimate of the number of reproductively successful individuals exchanged among local populations each generation (*Nm*). Estimates of gene flow in combination with the standardized variance of allele frequency (F_{ST}) can determine the genetic structure of natural populations (Barton and Slatkin 1986).

Social organization in New World quail results in populations subdivided into coveys (Johnsgard 1973). In the Northern Bobwhite (*Colinus virginianus*), coveys normally occupy a limited geographic area (Murphy and Baskett 1952, Lewis 1954). A predisposition to a cohesive, gregarious social organization and low functional vagility produce a social structure distinctively different from the majority of avian species examined electrophoretically (Matson 1984).

We attempted to determine if the unique social system and sedentary nature of bobwhites alter the partitioning of genetic variance within and among local populations (i.e. promote genetic subdivision). We estimated from allozymic data components of genetic variance and levels of gene flow among three natural populations of Northern Bobwhites from southern Illinois.

Bobwhites ($n = 122$) were live-trapped from three primarily agricultural areas in southern Illinois in autumn 1983. Two sites were on Crab Orchard National Wildlife Refuge (Area 3, $n = 85$, and Area 13, $n = 12$) in Williamson County; the third was on Southern Illinois University-Carbondale properties (SIU; $n = 25$) in Jackson County. Area 3 (85 ha) and Area 13 (263 ha) were 4.8 km apart and were effectively separated by Crab Orchard Lake. The lake's minimum intershore distance in this vicinity was ca. 1 km, and the minimum between-area distance around the lake's perimeter was 11.7 km. The SIU site (290 ha) was 17.3 km distant. The three areas were not hunted and supported estimated autumn densities of ≥80 birds/100 ha.

Captured quail were held at the Illinois Department of Conservation Game Farm, Mt. Vernon, Illinois. Blood (0.5-1.0 ml) was drawn from the brachial vein in 1-ml heparinized tuberculin syringes with 25-gauge, 15.9-mm needles. Blood samples were stored on ice in heparinized 3-ml evacuated containers and then processed according to Manlove et al. (1975). Undiluted plasma and erythrocyte hemolysate were stored at −70°C.

Horizontal starch-gel electrophoresis (Selander et al. 1971, Harris and Hopkinson 1976) was used to resolve 19 presumptive genetic loci. Buffer systems employed to visualize specific proteins (designated according to McAlpine et al. [1987] and followed by International Union of Biochemistry [1984] EC numbers) were as follows: (1) citrate-phosphate, pH 5.9 (Hopkinson and Harris 1969)—acid phosphatase 1 (ACP1;3.1.3.2), aldolase A, fructose-bisphosphate (ALDOA;4.1.2.13), and hemoglobin (HB); (2) continuous tris citrate II (Selander et al. 1971)—adenylate kinase 1 (AK1;2.7.4.3), creatine kinase (CK;2.7.3.2), glucose-6-phosphate dehydrogenase (G6PD;1.1.1.49), lactate dehydrogenase A,B (LDHA,LDHB;1.1.1.27), malate dehydrogenase, NAD (soluble) (MDH1;1.1.1.37), and phosphogluconate dehydrogenase (PGD;1.1.1.44); (3) lithium hydroxide (Selander et al. 1971)—esterase

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