

AGE-SPECIFIC SURVIVAL IN BREEDING BLACK-CAPPED CHICKADEES (*PARUS ATRICAPILLUS*)

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ABSTRACT.—I followed the survival of 153 Black-capped Chickadees (*Parus atricapillus*; 68 males, 85 females), which had bred at least once in or near my study area. All were of known age, and had been banded during a 10-year period, (1980–1981 through 1989–1990). Male breeders lived an average of 3.19 ± 1.85 years ($n = 68$), while female breeders averaged 2.53 ± 1.98 years ($n = 85$). Most of this difference was due to differential mortality during and immediately after their first breeding season; female breeders suffered a significant peak in mortality during this period, while males showed no particular peaks in mortality associated with any given season or age class. Two factors had a significant effect on female survival in their first breeding season: high initial rank in the previous winter's nonbreeding flocks; and being mated to a male with prior breeding experience. Moreover, oversummer mortality of young females mated to inexperienced males was significantly higher in years with cold spring weather (mean low temperature in May 7°C or below) than in years with warmer spring weather (mean low in May $>7^{\circ}\text{C}$). This suggests that inexperienced males may provide less food for their mates during egg laying and incubation than do experienced males, and that the effect on females of lower provisioning by inexperienced males is worsened by harsh weather conditions. The relationship between provisioning level and male experience also may carry over to the nestling period. The cost to a female of producing a particular brood size will, therefore, vary both with her own status and with the degree of experience of her mate. Hence, the relative cost of increased fecundity should vary from population to population, depending on the local proportion of young females and experienced breeding males. Received 18 July 1994, accepted 4 January 1995.

AN ENORMOUS literature exists on the possible costs of avian reproduction (e.g. Partridge and Harvey 1985, Gustafsson and Sutherland 1988, Pettifor et al. 1988, Linden and Møller 1989, Nur 1990). Evidence of reproductive cost can be derived from several approaches. One is food-supplementation studies; for example, female Mountain Bluebirds (*Sialia currucoides*) that received no supplemental food during the nestling period lost an average of 3 g during that period, while supplemented females showed no such loss (Garcia et al. 1993). Another very effective approach involves clutch or brood manipulation (Hegner and Wingfield 1987, Korpimäki 1988, Dijkstra et al. 1990). For example, European Kestrels (*Falco tinnunculus*) that received artificially increased broods showed lower nestling and parental survivorship than those with unchanged or smaller broods (Dijkstra et al. 1990). However, these studies are not easily interpreted and can lead to conflicting results. Nur (1984, 1988) published extensively on reproductive costs as shown by brood manipulations on Blue Tits (*Parus caeruleus*) and concluded that reproduction imposes signifi-

cant costs, especially on females. However, Pettifor (1993) reanalyzed Nur's data, along with three additional years of data on brood manipulations, and found no strong evidence of a cost of reproduction in Blue Tits, measured either as an increase in mortality or a decrease in fecundity of parents given additional young to rear.

This apparent contradiction can be explained by the fact that various factors can serve to mask reproductive costs. One such factor is seasonal variation; in studies conducted under particularly favorable conditions, reproductive costs might well be masked. This is best countered by long-term studies (e.g. Perrins and McCleery 1989), or by comparing responses in more- versus less-favorable habitats (e.g. Kluyver 1961). However, if certain age classes within a breeding population are less capable of bearing reproductive costs, the age structure of the breeding population itself might affect whether a study of that population would reveal such costs. Reproductive costs also can be masked by phenotypic optimization (Perrins and Moss 1975, Pettifor et al. 1988, Pettifor 1993). Finally, an-

other confounding variable is status, most easily measured by the winter rank of individuals that later become breeders.

I present evidence from my study that low-ranked young females are particularly vulnerable to the costs of reproduction, and that this is exacerbated, for young females of any rank, when they are paired with inexperienced males. The Black-capped Chickadee (*Parus atricapillus*) is ideal for long-term studies in that it is resident and highly sedentary; individuals, after juvenile dispersal, typically remain in the same general area for the rest of their lives (Odum 1942, Glase 1973, Smith 1991, 1994). Over a 10-year period (1980–1981 through 1989–1990), I evaluate survivorship of those chickadees banded as hatching-year (HY) birds that became breeders in or immediately adjacent to my study area.

STUDY AREA AND METHODS

The study area is 35 to 40 ha of a mixture of old field, second-growth mixed woodland, and residential area (described in detail by Smith 1994). During the 10-year period, this area supported an average of $57 \pm \text{SE of } 5.7$ resident chickadees each year: 46.6 ± 6.7 flock regulars; and 10.4 ± 4.5 winter floaters (Smith 1984, 1987, 1994). The flock regulars (i.e. birds that spend most or all of their time within the home range of a single winter flock) were organized into four to eight flocks ($\bar{x} = 6.1 \pm 1.3$).

Chickadees, captured in mist nets, were aged by skull pneumatization when appropriate (Yunick 1980, 1981) and also by tail-feather shape (Laaksonen and Lehtikoinen 1976, Meigs et al. 1983). Each bird received a unique color combination of up to four bands (two per leg), permitting identification at a distance. Birds were sexed by a combination of factors: wing length (Smith 1991), behavior, and relative dominance. First-year males typically do more body-ruffling displays (Piaskowski et al. 1991), and give more *gargle* vocalizations in the fall (Ficken and Weise 1984) than do young females. In relative dominance, HY birds able to supplant an after-hatching-year (AHY) female usually are male, while young birds unable to supplant an AHY bird almost always are female (Smith 1991).

Field data were taken usually three to six times per week from mid-August through the end of May, and about once every two weeks during June and July. Dominance hierarchies of all central study flocks were determined, as well as those in some neighboring flocks (details in Smith 1994). After flock break-up each spring, the breeding territories were mapped, and most of the nests, all of which were in natural sites, were found.

During the 10 years, I banded 561 chickadees in the study area. These included "migrants" (in irruption years), some members of peripheral flocks, and the resident birds (regulars and floaters) associated with the central study flocks. Of these, 153 birds (68 males and 85 females), all banded as HY birds, became breeders in or immediately adjacent to my study area.

RESULTS

Birds I report here as having died by one year of age, disappeared during April, May and June; those dying by 1.25 years were last seen in July, August or September. These two periods include the entire breeding season plus much of the postnuptial molt (Smith 1991).

Overall survivorship of breeders.—Figure 1 shows the mortality of all 153 breeders, separated by gender. The major difference between the two curves is during the birds' second summer and very early fall (ages 1.00 and 1.25). In fact, significantly more female breeders (35.3%) than males (17.6%) died during this period ($X^2 = 5.97$, 1 df, $P < 0.025$). This difference in survival reflects a consistent pattern, not just the result of one or two unusual years. Female oversummer mortality was greater than that of males in 8 of the 10 years (Table 1).

Of the 30 females that died by the end of their second September (age 1.25), 9 were alive in late August and/or early September. The remaining 21 include 3 that died in early May before incubation had begun, 1 that died during the nestling stage, and 17 that were last seen in late May or early June; it is unknown whether these vanished before or after the fledging of their offspring.

Factors affecting female oversummer mortality.—One factor that might have affected which females died prior to their second winter, and which survived, is their initial rank in the non-breeding flocks during their first winter. Of 85 breeder females, 19 had started their first non-breeding season as winter floaters (Smith 1984, 1987). This complicates the picture, as each successful floater must have had two winter ranks: initially very low (below all regulars of their sex), when they moved from flock to flock; and far higher after they settled into a flock by replacing a high-ranked regular member that had died (Smith 1984, 1987).

Therefore, I eliminated the 19 female floaters from this particular analysis, and assessed only the 66 female breeders that had entered winter

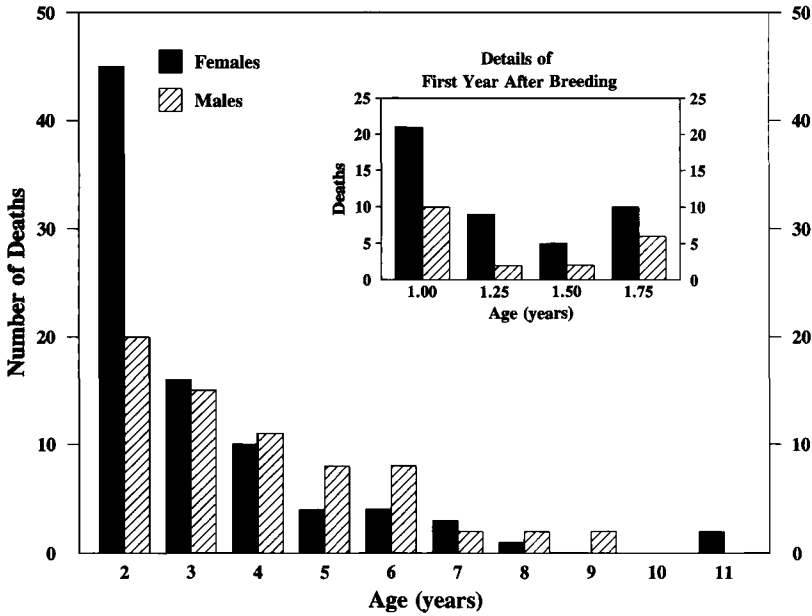


Fig. 1. Mortality of male and female Black-capped Chickadee breeders, starting with their second year of life (i.e. the first year after becoming breeders). Insert gives details of this critical year, separated into quarters: first quarter ends 30 June, second on 30 September, third on 31 December, and fourth on 31 March. Most of difference between male and female mortality occurred in first two quarters. Female mortality by end of September (1.25 years) was significantly greater than male mortality during same period.

flocks as regular members. I found that 23 of these 66 females died by age 1.25, and 43 survived. Of the 23 that died, only 5 (21.7%) had settled into their flocks ranked first or second among females; the rest (78.3%) were third-ranked or below. By contrast, 55.8% of the females that lived to be over 1.25 had entered

their first-winter flocks ranking first or second among females. This difference is highly significant ($X^2 = 7.05, 1 \text{ df}, P < 0.01$).

Another possible factor affecting whether females survive past 1.25 is the quality of their breeding partner. One way this could be assessed is by considering his rank during the previous winter. Although a female's rank typically reflected that of her mate in my study area (Smith 1984), the rank of their mates seemed to have no significant effect on female survivorship past their first breeding season ($X^2 = 1.56, 1 \text{ df}, \text{ns}$). Possibly, this is because 11 females lost their original mates over the winter and, thus, had to breed with other, different-ranked mates the following spring.

The quality of breeding partner also could be reflected by his relative experience. Thus, I compared young females paired with inexperienced (first-year) versus experienced (second-summer or older) males to evaluate what effect this might have on female survivorship over their first breeding season. Thirty-seven of the 85 females first bred with first-year males; of these, only about one-half (18) survived past 1.25 years. However, 75% of the 48 females that

TABLE 1. Oversummer mortality of yearling Black-capped Chickadee breeders.

Year	Females		Males	
	No. joining breeding population	Percent dying by September	No. joining breeding population	Percent dying by September
1981	7	28.6	6	16.7
1982	10	50.0	6	0.0
1983	7	14.3	7	42.9
1984	11	27.3	12	16.7
1985	7	14.3	4	25.0
1986	7	14.3	5	0.0
1987	5	80.0	5	0.0
1988	10	50.0	6	16.7
1989	10	40.0	11	27.3
1990	11	36.4	6	16.7

TABLE 2. Effect of mate's experience on oversummer mortality of yearling female Black-capped Chickadee breeders.

Year	Inexperienced mates		Experienced mates	
	Died	Survived	Died	Survived
1981	2	2	0	3
1982	5	1	0	4
1983	1	2	0	4
1984	2	3	1	5
1985	1	2	1	3
1986	0	1	1	5
1987	2	1	2	0
1988	2	1	3	4
1989	2	3	2	3
1990	2	2	2	5
Total	19	18	12	36

first bred with older males survived past 1.25 years; this difference is significant ($X^2 = 5.12$, 1 df, $P < 0.025$; Table 2).

To explore this further, I evaluated oversummer survival of older females (age two years and above) with respect to the relative age of their breeding partners. Of the 12 instances where older females bred with young, inexperienced mates, 5 (42%) died over that summer. However, of 50 instances where older females bred with older, experienced mates, only 8 (16%) died over that summer ($X^2 = 4.17$, 1 df, $P < 0.05$). Thus, prior breeding experience of a female's mate seems to have had a significant impact on oversummer survival of both young and older females.

One possible way in which male experience might affect females is in level of "courtship" feeding during egg laying and incubation. In cold springs, low levels of such feeding might be particularly hard on breeding females, since they depend on this provisioning for much of their energy intake at this time (Smith 1991). Mean low temperatures in May (when most of laying and incubation occurs in western Massachusetts) were below 7°C in four years (range

4.4°–6.9°) and above 7°C in the other six years (range 7.4°–10.2°). In the years when May lows were above 7°C, about one-half (42.1%) of the 19 young females that died over the summer bred with inexperienced males; however, in the years when May lows averaged below 7°C, 91% of the 11 females that died over the summer had bred with inexperienced mates (X^2 with Yates' correction = 5.03, 1 df, $P < 0.025$). Hence, having an inexperienced breeding partner had significantly more impact in years with cold springs than with warmer springs.

Effects of these factors on male mortality.—In male breeders, neither initial rank nor experience of breeding partner had any significant effect on oversummer mortality. Male flock members with initial rank of 1 or 2 during their first winter survived past 1.25 years no better than did males ranked 3 or below ($X^2 = 1.18$, 1 df, ns). As for experience of breeding partner, males whose initial mate was inexperienced actually survived past 1.25 years no better (85.1% of 47) than did males mated first to experienced females (76.2% of 21; $X^2 = 0.804$, 1 df, ns).

Breeder longevity.—Overall, males, once they became breeders, lived to an average of 3.19 years old; females, once breeders, lived to an average of only 2.53 years (Table 3). However, for birds surviving past their first breeding season, the averages converged; once chickadees had lived for two winters, both males and females lived, on average, to be 3.97 years old (Table 3).

DISCUSSION

Survivorship of male breeder Black-capped Chickadees was fairly uniform; there was no major mortality associated with any particular season or age class. Female breeders, by contrast, showed significantly higher mortality than males during and immediately after their first breeding season (Fig. 1).

Two factors were significantly correlated with

TABLE 3. Average life-span (years; $\bar{x} \pm$ SD with n in parentheses) of breeder Black-capped Chickadees calculated over four time intervals.

Time interval	Males	Females
From date of joining first fall flocks	3.19 \pm 1.85 (68)	2.53 \pm 1.98 (85)
After first breeding season (1.25 years old and older)	3.57 \pm 1.74 (58)	3.04 \pm 2.04 (64)
After 1.5 years	3.66 \pm 1.76 (56)	3.33 \pm 2.06 (55)
After two winters	3.97 \pm 1.63 (48)	3.97 \pm 2.10 (40)

female survival over their first breeding season. One was initial rank in the previous winter flocks; females highly ranked during the winter had much higher survival until the following September than did lower-ranked females. Winter rank possibly affects a bird's energy reserves, and birds with lowest reserves might be least equipped to meet the energy costs of breeding.

Survival of female breeders also was significantly affected by the relative experience of their mates; both young and even older (and thus relatively high-ranked; Glase 1973, Smith 1991) females with experienced breeding partners survived the summer significantly better than those with inexperienced mates. Hence, the inexperience of the male itself affects survivorship of the female.

In Black-capped Chickadees, as in many other species, females do all nest building, incubation, and brooding of the young. Females of many species commonly lose mass during incubation (Martin 1987, Johnson et al. 1990), although some claim this loss is an adaptation, rather than related to stress (e.g. Freed 1981). Several studies have found that the daily energy expenditure of breeding females is considerably lower during incubation than during the nestling phase (e.g. Finch 1984). However, most studies showing relatively low incubation costs have been done in relatively warm locations.

Two factors can increase incubation costs. One is temperature: the colder the ambient temperature, the more costly the process of incubation (Haftorn and Reinertsen 1985, 1990, Piersma and Morrison 1994, Wiggins et al. 1994). The other is clutch size, in that the larger the clutch, the more it costs to incubate (Biebach 1981, 1984, Haftorn and Reinertsen 1985, Martin 1987).

If low temperatures increase incubation costs, one might expect females simply to delay reproduction until temperatures are warm enough for incubation costs to be minimal; indeed, young female Black-capped Chickadees tend to lay clutches slightly later than do older chickadees (Smith 1991); the same is true of several other parids (Perrins 1979, Jarvinen 1991). However, female Black-capped Chickadees also experience strong selective pressure to begin laying as soon as possible. Glase (1973) found that the first HY chickadees to arrive in an area settled at higher ranks than did later arrivals; this also is well documented in Marsh Tits (*P.*

palustris; Nilsson and Smith 1988, Nilsson 1989a, b). Moreover, in most Black-capped Chickadee populations, not all chickadees that survive the winter manage to breed locally; usually, the lowest-ranked pairs in the flocks are driven away and have considerably lower chances of breeding anywhere at all (Smith 1967, 1984, 1991, Desrochers et al. 1988). Clearly, young that fledge earliest in the spring also will be the first to disperse and settle. These will join the newly forming flocks at higher initial ranks than will later-fledged birds, which will increase their chances of entering the breeding population the following spring.

In Black-capped Chickadees, as in many other species, a considerable portion of a female's food during nest building, egg laying and incubation can be brought to her by her mate. Numerous studies have shown that this provisioning has a major impact on the physical condition of the female (e.g. Lyon and Montgomerie 1985, Martin 1987). Significantly, in at least some species, such as the Pied Flycatcher (*Ficedula hypoleuca*), experienced males feed their incubating mates considerably more frequently than do inexperienced males (Lifjeld and Slagsvold 1986). Black-capped Chickadees may well do the same. This is suggested by the fact that the impact of having an inexperienced breeding partner on female oversummer survival was significantly greater when it was colder in May than when it was warmer.

Prior experience also may affect how much food a male parent brings to the nest once the young have hatched; for example, Saetre et al. (1995) found that older male Pied Flycatchers were more successful at feeding young than were year-old males. I have reexamined data on feeding rates at seven first-brood Black-capped Chickadee nests in eastern Massachusetts (Smith 1976). During days 2 to 10 posthatching, when male chickadees bring most of the food to the nest (Odum 1941, Smith 1991), the four nests provisioned by old males averaged of 71.29 mg/nestling each hour, while the three nests of inexperienced males averaged only 46.27 mg/nestling each hour. Sasvári (1986) has shown that low levels of help in feeding offspring can significantly lower the mass of parents in both Great Tits (*P. major*) and Blue Tits; the same is likely true in other parids as well.

Thus, female Black-capped Chickadees with inexperienced breeding partners likely receive less provisioning not only during incubation

but also during the early nestling phase (the period when females must brood young). This would increase the reproductive cost to such females.

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