

deserts and semi-deserts. Ecosystems of the world. Vol. 5, Ch. 13 (N. E. West, ed.). Elsevier, Amsterdam, The Netherlands.

WILLOUGHBY, E. J. AND T. J. CADE. 1964. Breeding behaviour of the American kestrel (Sparrow Hawk). *Living Bird* 3:75-96.

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Wilson Bull., 104(2), 1992, pp. 338-342

Pairbond persistence and "divorce" in Black-capped Chickadees.—Pairbond persistence over several years is common among parids including Black-capped Chickadees (*Parus atricapillus*; Odum 1942, Glase 1973); Carolina Chickadees (*P. carolinensis*; Brewer 1961, Dixon 1963); Mountain Chickadees (*P. gambeli*; Dixon 1965); and Plain Titmice (*P. inornatus*; Dixon 1949) in North America, and also in many European species, including the Great Tit (*P. major*; Hinde 1952) and others (reviewed in Perrins 1979). Occasionally, however, members of intact pairs may split up to form new alliances; Hinde (1952) and others have referred to this as "divorce." Among birds, divorce occurs when one member of an intact pair (two birds that bred together the last time breeding was possible) deserts its former mate to form a new pairbond with another bird; thus only birds that are at least one year old can be involved in divorce. Consequently, in birds such as Black-capped Chickadees, few, if any, birds with low winter rank can be involved in this process, since the vast majority of such birds (at least in most parid populations, including the chickadees in my study area) are less than one year old. In every divorce that I have observed, one bird moves and the other stays; I will consider the one that moves to be the bird that initiated the divorce.

This paper will examine all instances of divorce so far recorded in a small, color-banded population of Black-capped Chickadees in western Massachusetts, which I have been studying since the fall of 1979. During this time, the central winter population has varied from four to seven flocks, and the central breeding population, from 12 to 16 pairs (Smith 1988a, Smith 1991). This study population is not isolated physically from adjacent flocks or pairs, and for the purposes of the present paper, I also include data from banded members of peripheral chickadee groups.

Over the past ten years, I have recorded 15 instances of divorce among color-banded chickadees. During this same time period, 79 other intact pairs (just over 84%) remained together. Of the 15 divorces, 10 were initiated by females and five by males. Three of these divorces occurred during winter; six occurred in spring (April and early May), and six occurred in late summer. All six of the spring divorces were early enough to permit breeding by the newly formed pair; by contrast, all of the summer divorces occurred too late for breeding to take place that year.

Fourteen of the 15 records involved clear rank increases for the divorce initiators (Table 1). Each male initiator went from beta to alpha male. Eight of the 10 female initiators went from second-ranked female to highest-ranked (in my study area, over the last 10 years, female winter rank has consistently reflected that of her mate; hence the top-ranked female is paired to the flock's alpha male). One female moved from third- to second-ranked female. Finally, one female (AIK KR; see Table 1) went from top-ranked female of a four-bird flock to top-ranked female of an eight-bird flock. Since most males rank above females during the nonbreeding season, a four-bird flock's highest-ranked female would rank above only one bird, whereas an eight-bird flock's highest female would rank above three other birds.

TABLE 1
DIVORCES: WINTER RANKS AND FLOCKS

Individual	Original rank ^a	New rank ^a	Birds from same or different flocks	If different, new pair joins flock of
Female initiators				
A1Y RB	2	1	same	—
A1O GK	2	1	same	—
A1R BB	2	1	same	—
A1R OB	2	1	same	—
A1Y YB	2	1	same	—
A1G BY	2	1	same	—
A1Y RO	2	1	same	—
A1K YY	3	2	same	—
A1R RK	2	1	different	female
A1K KR	1	1	different	(she died that summer)
Male initiators				
YG	2	1	same	—
A1R OO	2	1	same	—
A1G KO	2	1	same	—
A1K KK	2	1	same	—
A1R GY	2	1	different	female

^a Within-sex rank in winter flock.

All but three new alliances involved members of the same flock (Table 1). The three between-flock alliances were all between members of two adjacent flocks. Somewhat surprisingly, of these three new pairs, the two that survived until flock formation (after first breeding together) both joined the female's home flock the following fall (Table 1). Both of these divorces were initiated in early spring.

All 15 divorces appeared to be triggered by the death of a high-ranked bird. The three winter records, all occurring before the winter of 1987–1988, were each instances of complex substitution: here a member of a flock's alpha pair dies, and is replaced by a member of the beta pair (the divorce), after which a winter floater settles into the beta pair, replacing the divorce initiator. Immediately after every winter divorce, each initiator not only seemed to associate extremely closely with its new mate, but also seemed actively to avoid the whereabouts of its former mate, which itself was associating very closely with a newly inserted winter floater (Smith 1984). From 1987–1988 on, however, the overall density of winter floaters in my study area has dropped considerably, and rapid replacements following winter mortality are now rare (Smith 1990). Therefore, most high-ranked chickadees that died during subsequent winters have not been replaced until the following spring, even when divorce was involved (see Smith 1990 for association index data). Hence the spring divorces include some cases of replacing high-ranked birds that have died four or five months earlier. Similarly, the summer records all appear to have occurred at the beginning of autumn flock formation, even if the death that triggered the divorce had occurred a month or two earlier.

Twice as many divorces were initiated by females as by males, although female mortality was not twice that of males during the same period. This is particularly true for winter and spring records. Looking only at mortality within the top-ranked pairs of each flock, male

TABLE 2
CHICKADEE DIVORCES: PAIRBOND PERSISTENCE

Sex of initiator	Year	Years with former mate	Years with new mate	Terminated by
F	1983	1 + ^a	1	Her death
F	1983	1	1	His death
F	1985	1	2	His death
F	1986	1	2	Her death
F	1986	1	1	His death
F	1988	1	1.5	Her death
F	1988	2	1	His death
F	1989	2	2 + ^b	(intact)
F	1989	1	2 + ^b	(intact)
F	1991	1 + ^a	1 + ^b	(intact)
M	1981	2 + ^a	1	Her death
M	1986	1	5.8	Her death
M	1988	1	2	His death
M	1990	1	1 + ^b	(intact)
M	1991	2	1 + ^b	(intact)

^a Banded as an adult.

^b Both still alive.

and female mortality from the end of August through the first week in May was identical over the ten years (16/66 for each sex), yet six females and only three males initiated divorces (winter and spring data combined). Nevertheless chi-square analysis reveals that these ratios do not differ significantly, possibly due to small sample sizes.

Chickadees that initiated one divorce were not likely to initiate another; indeed, each of the 15 divorces was initiated by a different bird, and every new alliance ended so far has been terminated by death, rather than by desertion (Table 2). Moreover, at least six of the new alliances persisted for at least two years, and one actually lasted for almost six years (Table 2).

As any bird grows older, it may passively increase its rank, due to increased age and/or mortality of other, higher-ranked birds. To examine whether the gains in rank of divorce initiators were any different from those their contemporaries gained through more passive means, I compared divorce initiators with non-initiators of the same sex, rank, flock size, and approximate age (I counted each bird only once). For winter divorces I examined final ranks at the end of that winter; for spring and summer divorces I compared initial rank in the previous winter with starting rank in the next winter's flocks. Fourteen of my initiators started at beta or below; all moved up in rank. By contrast, of 39 non-initiators starting at equivalent ranks, and surviving long enough to be assessed, only 12 increased their dominance, while 27 did not. Initiating a divorce was thus significantly more efficient at improving rank than was more passive behavior ($\chi^2 = 19.74$; 1 df).

Unfortunately, I do not have nest success data, so I cannot say how many, if any, of the spring and late summer divorces are correlated with poor nesting success. This is a possible alternative explanation, especially for late summer divorces. However, every one of the 15 divorces, including those initiated in late summer, resulted in the initiator ranking above more individuals than it had formerly. The more birds a chickadee ranks above at the

beginning of the nonbreeding season, the better its chances of avoiding ending the winter as the lowest-ranked bird of its sex (or indeed of the flock). This is particularly important for females, which rank below most males in the winter. Most (13/15) divorces involved moving from second- to top-ranked position within the bird's sex. For males, the advantages of becoming alpha in their flock are many. Some of the more obvious ones include preferential access to the best foraging sites, both in terms of food quality and safety against predators (see, for example, Ekman and Askenmo 1984, Desrochers 1989). Alpha males are also much more likely to be sought out for extra-pair copulations (Smith 1988b), and indeed, as the present paper shows, they are also less likely to be deserted through divorce than are beta males. Both members of a top-ranked pair are assured of obtaining a local breeding territory, which, in many parts of this species' geographic range, is not always possible for lower-ranking pairs (Smith 1967, 1984; Desrochers et al. 1988). Moreover, this territory is likely to be the best quality available (Smith 1976). Females that become paired to alpha males also gain a rather subtle but important advantage, documented by Ekman (1990) for Willow Tits (*Parus montanus*). He showed that females paired to dominant males were subject to aggression less often than expected, due to increased protection by their (alpha) mates. M. L. Withiam, D. Lemon, and C. P. L. Barkan (pers. comm.) have obtained similar data for Black-capped Chickadees.

Both sexes can initiate divorce. Even though twice as many females as males initiated divorces during a period when identical number of top-ranked vacancies occurred, this difference was not statistically significant. Future research is needed to see if there is truly no difference between males and females, or if, alternatively, females are actually more likely than males to seek out new, higher-ranking alliances.

Acknowledgments.—This paper has benefited considerably from reviews by K. Dixon, J. Hailman, and C. Weise.

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Wilson Bull., 104(2), 1992, pp. 342–345

The effectiveness of Helmeted Guineafowl in the control of the deer tick, the vector of Lyme disease.—Lyme disease, a parasitic infection of increasing concern in the United States, is caused by a spirochete (*Borrelia burgdorferi*) spread by the deer tick (*Ixodes dammini*, Acarina, Ixodidae; Lane et al. 1991). A variety of measures for controlling the deer tick has been suggested, such as pesticides, burning, host eradication, or removal (Mather et al. 1987, Schulze et al. 1987, Wilson et al. 1988), but no single method has been demonstrated to be effective over a wide variety of habitats. Use of certain pesticides (Stone 1979) and host eradication, especially of the white-tailed deer (*Odocoileus virginianus*, Wilson et al. 1988), are not practical near areas of heavy human use such as playgrounds, school yards, and suburban housing developments.

The Helmeted Guineafowl (*Numida meleagris*) has been used as a “folk” defense against ticks acting as vectors for Lyme disease on Shelter Island, New York, and on the islands of Martha’s Vineyard and Nantucket, Massachusetts. In Africa, this species eats a wide variety of arthropods (Skead 1962, Angus and Wilson 1964, Grafton 1971, Mentis et al. 1975) and gleans ticks from warthogs (*Phacochoerus aethiopicus*; Maclean 1984). In the United States, Crowe (unpubl. data) found ticks in the stomachs of three Helmeted Guineafowl in Nantucket.

Accordingly, we tested whether guineafowl might be useful in reducing tick populations in a series of controlled enclosure and enclosure experiments during September–November 1990 when adult deer ticks quest for large mammalian hosts (Daniels et al. 1989). Our experiments were performed at suburban sites in Easthampton, Suffolk County, New York, where free-ranging guineafowl had been introduced one year earlier to control high tick numbers, and in Islip, Suffolk County, New York, where guineafowl had not been present for ten years and tick populations previously seemed elevated (C. D. Webster, pers. comm.).

Although the deer tick is commonest in woodland (Maupin et al. 1991), we chose lawns because most human activity occurs on lawns and because people on lawns appear less likely to take precautions against ticks than when entering habitats such as woodlands (D. Duffy, pers. obs.). Lawns are also structurally more homogenous than woodland or hedgerow,