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# **The Ecology and Behavior of Chickadees and Titmice**

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**An integrated approach**

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# **Social dominance and fitness in black-capped chickadees**

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## **9.1 Introduction**

Dominance hierarchies mediate social interactions in many group-living animals (Piper 1997; Dugatkin and Earley 2004). Such hierarchies often emerge rapidly as the result of dyadic interactions between individuals over access to resources (Drews 1993; Beacham 2003). An individual's relative social rank may be influenced by characteristics such as personality (Dall *et al.* 2004), intrinsic resource-holding potential and experience (Hansen and Slagsvold 2004), as well as extrinsic, context-dependent features of competition such as group make-up (Wiley *et al.* 1999) and the value of resources (Dale and Slagsvold 1995). Although social rank, by definition, must always be a relative trait (Drews 1993), dominance hierarchies predominate in animal groups with stable membership; thus rank relationships are typically long-lasting (Wiley *et al.* 1999; Forkman and Haskell 2004). If acquiring and maintaining high status is costly (Hogstad 1987a; Hay *et al.* 2004), dominant birds should derive sufficient benefits from improved foraging, mating, or protection from predators to offset these costs (Ellis 1995).

Studies of the family Paridae (tits, titmice, and chickadees) have contributed important information to our understanding of passerine life histories (McCleery and Perrins 1988; Dhondt 1989; Blondel *et al.* 1990; Smith 1991). Many Parids spend the non-breeding portion of their annual cycle in flocks with linear dominance hierarchies and depend on food storage for winter survival (Ekman 1989; Lundborg

and Brodin 2003). Flock size, range, sex ratio, coherence, and stability of hierarchies vary within and between species (Hogstad 1989; Matthysen 1990; Smith 1991; Verbeek *et al.* 1999; Hay *et al.* 2004). Despite this variation there is abundant evidence that social rank within flocks influences individual success, as a result of differential access to food (Glase 1973; Hogstad 1987b; Desrochers 1989; Ficken *et al.* 1990; Smith 1991) and breeding partners (Smith 1988; Otter and Ratcliffe 1996; Mennill *et al.* 2004), as well as rank-related variation in predator avoidance (Zanette and Ratcliffe 1994; Koivula *et al.* 1996).

Black-capped chickadees are undoubtedly the best-studied of the North American Parids, yet data on long-term reproductive output are scarce (Smith 1991). Only one study (Schubert *et al.* in press) has evaluated the relationship between social rank and lifetime fitness. Chickadees are an ideal species for such a study (apart, perhaps, from the disinclination of black-capped chickadees to use nest boxes). They are broadly distributed across a range of temperate North American habitats. Like most other Parids, including the willow tit (Lahti *et al.* 1996), black-capped chickadees winter in dominance-structured flocks of three to 12 birds, in which males dominate females and mature birds dominate yearlings (Glase 1973). Flocks typically consist of two or more adult birds and one or more yearlings recruited from outside of the local population. Birds often breed with a member of their winter flock, and therefore chickadee flocks are sometimes described as a "hierarchy of pairs"

(Smith 1991). Once recruited, chickadees are highly philopatric, so the effects of winter social rank on breeding success and status in succeeding wintering flocks can be measured.

In this chapter we examine naturally- and sexually-selected consequences of social rank in a population of black-capped chickadees studied for over a decade in eastern Ontario, Canada. We begin by reviewing what is known about the characteristics that distinguish individuals attaining high social rank from subordinates. We describe aspects of status signaling, such as song and plumage features, as well as rank-related differences in survival and annual reproductive success. Using our extensive observations of interactions among color-banded individuals, we describe the process by which dominance hierarchies are maintained. We then review the effects of individual variation in rank acquisition on lifetime reproductive success (LRS). To date most studies of avian life histories, including the excellent work on great tits (McCleery and Perrins 1988) and blue tits (Dhondt 1989), have investigated phenotypic correlates of fitness, but few have examined how the dynamics of social rank acquisition influence LRS. Analysis of LRS permits us to compare how the overall genetic contribution of individuals is affected by both lifespan and reproductive strategies. Breeding lifespan has been identified as the most important predictor of LRS in mammals and birds (e.g. Clutton-Brock 1988; Newton 1989); nevertheless the interaction between social rank and LRS may also be significant and warrants investigation (Verhulst and Salomons 2004).

## 9.2 General methods

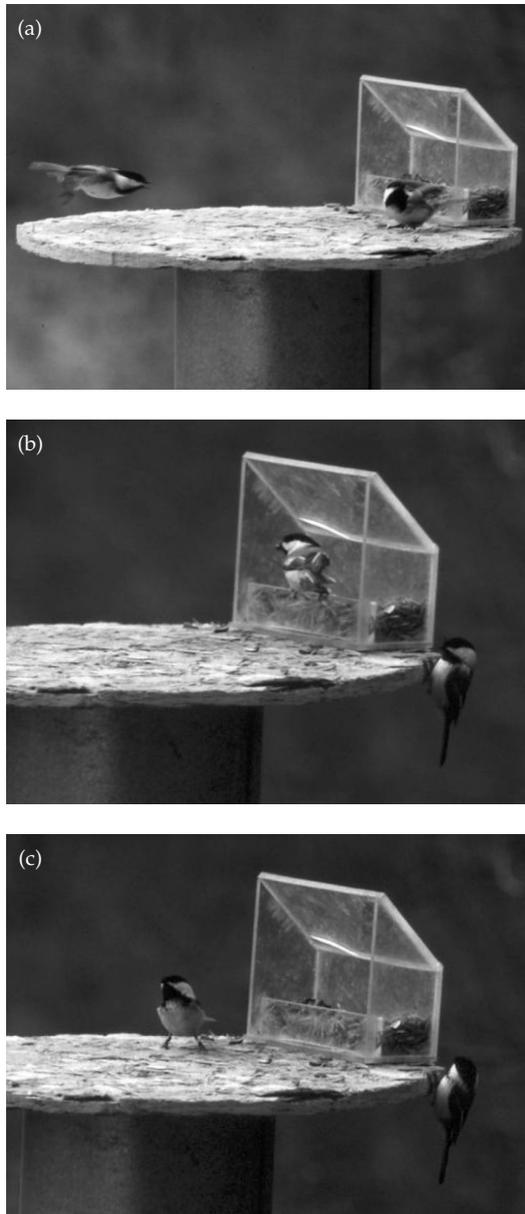
We have monitored black-capped chickadees at Queen's University Biological Station (QUBS), Chaffey's Lock, Ontario, Canada (44° 34'N, 76° 19'W) since 1987. The life history data reported here were collected from 1992 (initiation of breeding studies) through 2002. Data on winter dominance and flock memberships (but not flock formation) were collected from 1994 through 2002. During this period the 2-km<sup>2</sup> study site supported an average of  $17.2 \pm 2.1$  winter flocks and  $60 \pm 8.2$  breeding pairs per year. Mean flock size was  $5.5 \pm 0.1$  birds ( $N = 155$  flocks), smaller than

Smith's (1991) reported average of eight birds in western Massachusetts. Flock sex ratios were only slightly male-biased, averaging  $1.2 \pm 0.1$  males per female. Birds bred overwhelmingly in natural cavities (80% of nests; Mennill and Ratcliffe 2004a) rather than nestboxes. Field protocols as described below were similar across years (see Schubert *et al.* in press for full details of methods and data analysis).

### 9.2.1 Winter field methods

From January to March, birds were captured in baited Potter traps (average =  $146.8 \pm 12.5$  birds/winter) and individually marked with aluminum Canadian Wildlife Service bands and one to three colored plastic bands. Standard morphological measures (mass, tarsus, wing, rectrix length, fat score) and 10 to 80  $\mu$ l of blood were collected from each bird for sexing and paternity analysis. Birds were aged as second year (SY) or after-second year (ASY) using standard protocols and banding records (Mennill *et al.* 2004). Flock memberships were obtained by tracking flock movements across the site and scoring arrival times at feeders. Dominance relations among flock members were already well-established by the start of our observations each January.

We assessed dominance hierarchies within flocks by tabulating over 20 000 pairwise interactions (average of  $2439 \pm 712$  per year) between banded birds at feeding platforms which accommodated only one feeding individual at a time (Fig. 9.1). We inferred that an individual was dominant over an opponent when they: (i) supplanted or chased an opponent, (ii) resisted a supplanting attack by an opponent, (iii) elicited a submissive posture in an opponent, or (iv) fed while an opponent waited to approach the feeder (Ficken *et al.* 1990; Otter *et al.* 1998). These four types of interaction did not occur in equal proportion; the last two types of interaction occurred very frequently, supplants and chases occurred less often, and resisting a supplanting attack occurred very rarely. Hierarchies within flocks were ordered using MatMan software (Noldus Information Technology—see review by deVries 1998). Dominant (high-ranking) males were categorized as the male that held the top position in



**Figure 9.1** Photographs of dyadic dominance interactions in a wintering flock of black-capped chickadees. (a) A dominant individual (left) flies in to supplant a subordinate individual. (b) A dominant individual feeds while a subordinate individual waits to approach the feeder. (c) A dominant individual (left) elicits a submissive posture in his opponent (turning his head away from the dominant). Photographs by D. J. Mennill.

flocks with two or three males, and the top two positions in flocks with four or five males; subordinate (low-ranking) males held the bottom position or bottom two positions, respectively. In flocks with three or five birds, the middle bird was classified as “mid-ranking”. Most comparisons used these nominal categories, so sample sizes were based on numbers of flocks. In some cases, to allow comparisons across flocks, a continuous rank score for each bird (number of interactions won divided by total interactions) was also calculated (Mennill *et al.* 2004). Because dominance interactions occur at a lower rate and intensity between females than males, and their functional significance is still incompletely understood (Ramsay and Ratcliffe 2003; L. Ratcliffe, unpublished data), we have limited most analyses presented here to male rankings.

### 9.2.2 Spring field methods

Pairs were monitored from flock break-up (typically late March to early April) to determine territory boundaries and locate nest cavities. Breeding data were collected from a total of 536 pairings involving 294 males and 282 females. At approximately day 6 post-hatch, we collected 10 to 50  $\mu$ l blood from the tarsal vein of nestlings for paternity analysis (Mennill *et al.* 2004). Fledglings typically dispersed outside the boundaries of our study area, precluding accurate measures of recruitment. Thus we measured male realized reproductive success (RRS) as the total number of within- and extrapair nestlings sampled at day 6; female success equaled the number of offspring in the nest, since egg dumping was extremely rare (Otter *et al.* 1998; Mennill *et al.* 2004).

### 9.3 Correlates of social rank

Table 9.1 summarizes our current knowledge about the morphological, behavioral, and reproductive characteristics associated with social rank in black-capped chickadees. Here we review some of these features originally described by Smith (1991), and describe new ones which have emerged from our recent work. These findings provide good evidence of important variation in features that signal male quality and individuality. Undoubtedly future work will reveal additional examples.

**Table 9.1** Correlates of social rank in black-capped chickadees

Feature	Pattern	Reference
Age	Adults dominate juveniles No age effect in females	Smith 1991, Otter <i>et al.</i> 1999, Schubert 2003 Ramsay and Ratcliffe 2003
Sex	Males dominate females	Smith 1991
Seniority	Residents dominate intruders: Males Females  Early dispersing fledglings dominate later dispersers No effect of fledgling seniority	Smith 1991 Otter and Ratcliffe 1996, Ramsay and Ratcliffe 2003, S Ramsay and L Ratcliffe, unpublished Smith 1991 Leonard <i>et al.</i> 1991
Body condition	Dominant males and females leaner	Schubert <i>et al.</i> 2006, S Ramsay and L Ratcliffe, unpublished
Foraging	Dominants access more profitable, safer feeding sites	Desrochers 1989, Ficken <i>et al.</i> 1990
Predator responses	Dominants show less risky behavior (calls and movement)	Zanette and Ratcliffe 1994
Plumage	Dominant males have darker melanin (cap, mantle, bib), brighter white, and faster tail feather growth	Mennill <i>et al.</i> 2003a, Doucet <i>et al.</i> 2005, Woodcock <i>et al.</i> 2005
Song structure	Dominants better at transposing songs across species' frequency range	Christie <i>et al.</i> 2004
Singing behavior	Dawn chorus of dominants begins earlier in morning, lasts longer, higher song rate	Otter <i>et al.</i> 1997
Response to interactive "intruder"	Subordinates respond more agitatedly to playback, closer approach to speaker than dominants	Mennill and Ratcliffe 2004b
Response to simulated vocal duels	Dominants more likely to approach simulated winner	Mennill and Ratcliffe 2004c
Territory	Dominants out-compete subordinates for access Dominants have larger territories	Desrochers <i>et al.</i> 1988 Smith 1991, Mennill <i>et al.</i> 2004
Mate attraction	Dominant "widowers" attract new female sooner Dominant males more attractive to naïve females	Otter and Ratcliffe 1996, Smith 1991 Bronson <i>et al.</i> 2003, Woodcock <i>et al.</i> 2005
Divorce	Females desert mates for higher ranked males	Ramsay <i>et al.</i> 2000
Extrapair paternity	Extrapair males higher-ranked than social males	Smith 1988, Otter <i>et al.</i> 1994, 1998; Mennill <i>et al.</i> 2003b, 2004
Clutch size	Mates of dominant males more likely to lay eggs, have larger clutches and higher % hatch	Otter <i>et al.</i> 1999, Doucet <i>et al.</i> 2005
Nest success	Mates of dominant males incubate longer than mates of subordinates, feed nestlings less often, have higher nest survival and fledging success	Otter <i>et al.</i> 1999

### 9.3.1 Age

Smith (1991) observed that male social rank correlates with age class (ASY birds typically dominate SY birds), whereas a female's rank may better reflect that of her mate than her own age. Like Smith (1991), we have found that young (SY) males can, in some circumstances, dominate older birds (ASY; see below), but overall high-ranked males were significantly older ( $3.4 \pm 0.1$  years) than their subordinate

flock-mates ( $1.6 \pm 0.1$  years) ( $P < 0.0001$ ) (Schubert *et al.* 2006). Similarly, Otter *et al.* (1999) found that among 27 pairs of chickadees where intrasexual ranks and ages of both members were known, male age and rank were strongly correlated, but female rank was more strongly correlated with her mate's age and rank than her own age. In aviary-staged dominance contests between females, age by itself was also a poor predictor of winning (Ramsay and Ratcliffe 2003).

### 9.3.2 Sex

Males are dominant over females (Smith 1991). Although Smith (1991) reported that females may sometimes be dominant over males, we found this rarely occurred. Looking at a subset of our data, including 22 flocks from 2000 and 2001 where there was a clear hierarchy among both the males and females, we found that in 21 of 22 flocks the lowest-ranking male was dominant to the highest-ranking female. Our data therefore match those of Glase (1973) who found that males are quite consistently dominant over females. Interestingly, most cases where we observed females dominating males occurred between birds who ended up as breeding partners, where the male waited for his partner to finish feeding before approaching the feeder (interaction type iv, above).

### 9.3.3 Seniority

Prior residency is an important correlate of social dominance in tits during interactions at territory boundaries and during flock formation. However detailed studies of residency effects, especially in females, are rare. In captive great tits, residents dominate intruders, but adults—presumably more experienced—dominate juveniles when circumstances are unfamiliar to both (Sandall and Smith 1991). Smith (1991) found that chickadees removed from winter flocks for up to 4 days generally regained their former status. Our work shows that at the onset of the breeding season, females removed for up to 96 hours from their high-ranked mates easily evicted replacement mates (Otter and Ratcliffe 1996; S. Ramsay and L. Ratcliffe, unpublished data). In aviary contests, female “owners” out-ranked “intruders” (Ramsay and Ratcliffe 2003), as found in willow tits (Koivula *et al.* 1993). Thus although rank differences are more challenging to measure among females than males, females exhibit clear rank-related aggression outside the context of the pair bond.

Work with captive tits shows early experience may affect offspring dominance status (Hansen and Slagsvold 2004). Smith (1991) reported very low levels of aggression within chickadee families, with no clear pattern of dominance hierarchies among

fledglings. However she also suggested that earliest-dispersing juveniles were probably the most successful at joining flocks by pairing with widowed adults, with a correlated rise in status. Glase (1973) showed that juveniles with greater skull pneumatization (a reliable age indicator) in early fall were more likely to dominate later-arriving birds. In marsh tits, larger and more aggressive fledglings dispersed earlier than smaller fledglings regardless of sex (Nilsson and Smith 1985, 1988). In contrast, our studies of fledgling aggression and dispersal in eight chickadee family groups over the 22-day fledgling period showed aggressors were no larger than their victims, nor did they disperse earlier (although sample sizes were smaller than those in the marsh tit study; Leonard *et al.* 1991). We have not documented flock formation in our population, and thus the ontogeny of first-year rank remains an important area for future research.

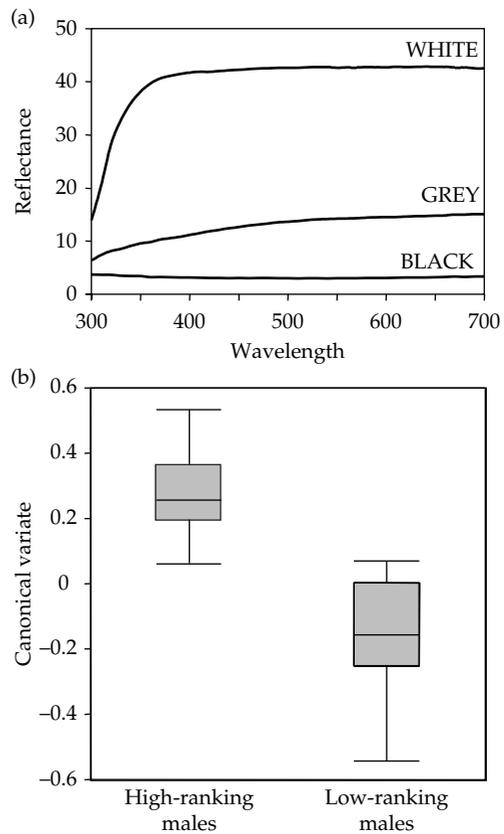
### 9.3.4 Size and condition

Because dominance is associated with preferential access to food and decreased risk of predation, it seems reasonable to predict that high-ranking birds carry fewer reserves than subordinates in winter when foraging conditions are challenging (Cresswell 2003; see also Chapter 3). Modeling the relation between dominance and mass (or condition) has turned out to be more complex than originally thought because of the need to consider variation in predation risk and environmental conditions (Lundborg and Brodin 2003; Ekman 2004), including flock stability (Lange and Leimar 2004). Neither Glase (1973) nor Smith (1991) found any compelling evidence that body size relates to dominance effects in chickadees (but see Hogstad 1987b); condition was not measured. However, in paired comparisons of the highest- and lowest-ranking males in flocks, Schubert *et al.* (2006) found dominant males had longer wings and tarsi, lower fat scores, and were in leaner condition than subordinates. Importantly, when age-matched flock-mates were compared, the differences in wing and tarsus disappeared but low-ranked birds were still heavier and had greater fat scores. Thus high-ranked males are leaner but not larger when age is taken into account. Similarly, in 15 field trials where

females mated to dominant males were removed for 86 to 94 hours prior to onset of egg-laying, the 12 females that were able to oust their replacements within a short time of being released and were, on average, leaner than replacements (S. Ramsay and L. Ratcliffe, unpublished data, but note sample size was insufficient to control for age effects). Overall, our results agree with most other studies of Parids showing dominance is not related to body size *per se* (Hay *et al.* 2004; but see Braillet *et al.* 2002 for population differences), whereas dominants tend to carry lesser weight reserves than subordinates (Pravosudov and Grubb 1997).

### 9.3.5 Plumage

Visual signaling in chickadees has attracted little attention compared to the better-characterized great and blue tits (Lemel and Wallin 1993; Lange and Leimar 2003; Alonso-Alvarez *et al.* 2004). The achromatic (black, white, grey) plumage of black-capped chickadees looks monomorphic to the human eye, as is described for many Parids. Smith (1991) surmised from her observations of dominance interactions that chickadees must be able to recognize the sex and relative social rank of others both quickly and accurately from considerable distances. We confirmed her prescient suggestion that there are substantial sex and rank differences in chickadee plumage features across the visual spectrum which are not detected by the human eye (Fig. 9.2a). Reflectance spectrometry of six body regions of chickadees captured in late winter flocks has revealed that not only are males brighter white than females, they also have larger black bibs and greater plumage contrast between adjacent white and black body regions. In addition, plumage variation is related to differences in social rank. High-ranked males have darker black caps, and differences in the color of their black bibs and grey mantles relative to their subordinates, independent of age (Fig. 9.2b). Measurements of growth bars in naturally-molted feather show dominant males also grow their tail feathers significantly faster than subordinates (Mennill *et al.* 2003a). This last finding contrasts with that of Hay *et al.* (2004) who found that dominant coal tits grew induced tail feathers more slowly than subordinates. The different



**Figure 9.2** (a) Average plumage reflectance spectra of the white cheek patch, the gray mantle, and black cap in black-capped chickadees (based on spectrophotometric measurements of 40 males) (from Doucet *et al.* 2005). (b) Association between male rank and achromatic plumage color. High-ranking males had high canonical variate scores, indicating darker black caps, grey mantles with proportionately greater reflectance at intermediate wavelengths, and black bibs with proportionately less reflectance at intermediate wavelengths (from Mennill *et al.* 2003a).

results may reflect effects of manipulating feather regrowth in the latter study. A subsequent study on our QUBS population has shown that the UV-chroma of these melanin-based features successfully predicts male realized reproductive success (within and extrapair offspring) (Table 9.2; Doucet *et al.* 2005). These data suggest that achromatic plumage provides reliable cues about sex and quality. Female chickadees exposed to unfamiliar males in aviary choice tests can identify dominant individuals rapidly without observing them

**Table 9.2** Significant plumage predictors of male reproductive success from multiple regression models constructed using a backward stepwise procedure

	R <sup>2</sup>	β <sup>a</sup>	df	P
<i>Apparent reproductive success</i>				
No significant predictors				
<i>Proportion of within-pair young</i>				
Whole model	0.65		2, 9	0.008
White brightness	0.38	1.01	1, 10	0.002
Melanin UV chroma	0.27	0.65	1, 10	0.03
<i>Overall realized reproductive success</i>				
Melanin UV chroma	0.20		1, 38	0.01

<sup>a</sup>Standardized partial regression coefficients.

Each model was constructed using four color variables (brightness of white patches, UV chroma of white patches, brightness of melanin-colored black patches, ultraviolet chroma of black patches), dominance rank, and body condition as potential predictor variables. Dependent variables (measures of male reproductive success) are shown in italic. Full details of analysis are presented in Doucet *et al.* 2005. Only plumage color variables were significant predictors of two measures of reproductive success.

interact, consistent with this hypothesis (Woodcock *et al.* 2005). Additional studies are needed to determine how individual and rank-based differences in plumage mediate competitive interactions in flock hierarchies. Achromatic plumage color may well provide “badges” of quality in aggressive, intrasexual encounters in chickadees, as does UV color in blue tits (Alonso-Alvarez *et al.* 2004).

### 9.3.6 Vocalizations

The two-note *fee-bee* song of chickadees functions in long-distance territorial communication, providing both male and female audiences with a rich array of cues correlated with the quality of the singer (see Chapter 14). Males can frequency-match rivals by transposing their single song type up and down a continuous frequency range. Such “pitch shifts” introduce fine structural changes in relative note frequency, amplitude, and duration. While the tendency to shift songs is not related to social rank, dominant males are superior singers, that is they maintain relative note stereotypy in shifted songs significantly better than low-ranking males (Christie *et al.* 2004). Dominants also begin the dawn chorus earlier, sing for longer, and sing at higher rates (Otter *et al.* 1997). In mock countersinging duels (playback from two loudspeakers at

the territory edge), dominant territory holders are more likely to approach the simulated “winner” (more threatening rival) than are subordinate territory holders (Mennill and Ratcliffe 2004c). When territory holders are themselves challenged with aggressive interactions via playback, dominants do not engage with the “intruder” as intensely as subordinates (Mennill and Ratcliffe 2004b). Engaging in intense song contests may be particularly costly for dominants, since they are unlikely to be cuckolded unless they “lose” in countersinging interactions with territorial intruders (Mennill *et al.* 2002). In a similar vein, dominants in winter flocks are risk averse, that is when exposed to predator models they take longer to call and break the freeze than subordinates (Zanette and Ratcliffe 1994).

### 9.4 Hierarchy formation and maintenance

Although the correlates of social rank have been well established through ongoing research, the process of hierarchy formation and the mechanics of hierarchy maintenance have received little attention. Several hypotheses have been proposed to explain how dominance hierarchies are formed and maintained (reviewed in Forkman and Haskell 2004). The *first fight hypothesis* maintains that

dominance relationships arise from an initial encounter between two individuals. The *continuous assessment hypothesis* maintains that multiple, ongoing interactions and challenges are responsible for developing and maintaining dominance hierarchies. As an extension of the continuous assessment hypothesis, the *suppression hypothesis* maintains that dominant individuals condition their subordinates to lose through ongoing attacks. Under the first fight hypothesis, the cost of an individual fight is expected to be high, and aggression is not necessarily expected to be greater between pairs of animals who hold adjacent rank positions versus pairs with non-adjacent rank positions. Under the continuous assessment hypothesis, the cost of an individual fight is expected to be low and aggression between pairs of animals should occur more frequently when they hold adjacent rank positions (i.e. when they have similar fighting abilities). Under the suppression hypothesis, the cost of an individual fight is expected to be low, and dominant animals should instigate aggressive encounters with their subordinates whereas the reverse should occur rarely (Forkman and Haskell 2004).

To better understand chickadee dominance hierarchy formation and maintenance, we tested the predictions of these three hypotheses using a dataset of 6234 dominance interactions between 278 birds from 48 flocks, collected in January to March of 2000 and 2001 in our eastern Ontario study population. Dominance interactions may be divided into interflock and intraflock interactions, and we focus on 3114 intraflock interactions to investigate the three hypotheses for the formation and maintenance of dominance hierarchies. Of these interactions, we observed 129 interactions that involved especially aggressive supplanting attacks. These highly aggressive interactions are particularly helpful for evaluating the predictions for these three hypotheses.

Is the cost of intraflock chickadee aggression high or low? Our observations suggest that the cost of aggressive encounters between flock-mates during the non-breeding season is low. For the 129 aggressive supplants that we observed, none appeared to lead to an injury in the dominant or subordinate bird. The primary cost associated with these

aggressive interactions appeared to be a temporary delay in access to food resources; in most observed cases the supplanted individual returned to the feeder shortly after the aggressive supplant. This low cost of aggression stands in contrast to the outcome of fights we have observed at other times of the year. In mid and late April, when flock hierarchies have dissolved and birds have begun defending territories, we have observed many aggressive encounters which have escalated to extended physical contact, sometimes resulting in lost feathers and, in a few cases, prolonged head injuries (noticeable as persistent swollen skin around the eyes). During the breeding season, we have observed such high-cost aggressive encounters occur between two males and, less frequently, between two females. From the onset of our studies at QUBS (K. A. Otter, personal communication) we have also observed a frequent form of aggression during the early breeding season in the form of "triangle fights", which occur as a low-ranking male persistently supplants and chases a high-ranking female in the presence of her high-ranking partner, who only occasionally steps in to harshly supplant the low-ranking male. These triangle fights rarely involve extreme aggression, but nevertheless appear to come at a high cost to the female, who can spend up to an hour practicing evasive maneuvers. Relative to these forms of aggression during the breeding season, aggression between flock-mates during the non-breeding period appears to come at a low cost.

Does aggression between pairs of individuals occur more frequently between individuals occupying adjacent rank positions? To answer this question, we focused on aggressive male–male interactions that occurred in flocks with three, four, or five males (in flocks with two males, all male–male interactions necessarily occur between birds with adjacent rank position). The highly aggressive interactions we observed did not occur between males with adjacent rank positions more often than expected by chance. In flocks with three males, 69% of highly aggressive interactions occurred between males with adjacent rank positions (binomial test against expected proportion of 66%:  $P = 0.68$ ,  $N = 13$ ); in flocks with four males, 46% of highly aggressive interactions occurred

between males with adjacent rank positions (binomial test against expected proportion of 50%:  $P = 0.42$ ,  $N = 26$ ); and in flocks with five males, 60% of highly aggressive interactions occurred between males with adjacent rank positions (binomial test against expected proportion of 40%:  $P = 0.91$ ,  $N = 5$ ). Therefore, our results do not support the second prediction of the continuous assessment hypothesis.

Do dominant birds instigate aggressive encounters? Of the 129 highly aggressive supplanting attacks that we observed in 2000 and 2001, we found that the overwhelming majority involved a dominant individual attacking a subordinate individual. For 58 aggressive supplants between males, 57 involved the dominant bird supplanting his subordinate flock-mate; for 11 aggressive supplants between females, 10 involved the dominant female supplanting her subordinate flock-mate; for 60 aggressive supplants between a male and a female, 58 involved the dominant bird supplanting their subordinate flock-mate. (Of the latter 58 supplants, 19 were cases where a male supplanted his own breeding partner.)

Taken together, these data provide support for the suppression hypothesis: the cost of an individual dominance fight appears to be low, and dominant individuals instigate aggressive encounters with their subordinates. In contrast to the prediction of the continuous assessment hypothesis, aggression does not occur between individuals holding adjacent rank positions more often than would be expected by chance. Further research is required to evaluate the cost of fights during initial encounters when birds first form flocks in the fall, so that we may better understand the importance of “first fights” in establishing position in chickadee dominance hierarchies.

#### 9.4.1 Consistency in dominance relationships between sites

Some bird species exhibit dominance relationships which are site-specific or context-specific, including Carolina chickadees (Smith 1991) and mountain chickadees (Dixon 1965; interactions between non-flock-mates were site-specific). Many European Parids show site-specific dominance relationships;

in both great tits and blue tits, dominance relationships depend on the proximity to the previous year's breeding territories (Colquhoun 1942; De Laet 1984). In contrast, winter dominance relationships within black-capped chickadee flocks are not site-specific. This has been reported qualitatively by Hartzler (1970) for a Minnesota population, Smith (1976) for a Massachusetts population, and Desrochers and Hannon (1989) for an Alberta population. Using dominance data from our eastern Ontario population, we attempted to quantify the consistency of chickadee dominance interactions across sites. Of 2257 dyadic, male–male dominance interactions we observed in 2000 and 2001, we found 27 dyads where the same two males interacted at two different feeder sites. The minimum distance between neighboring feeder sites at our Ontario study site is 175 m, and in all 27 cases, the two winter feeders were in positions that fell within two different birds' breeding territories in both the preceding and subsequent breeding seasons. Of the 27 dyads, there were 22 where the dominance relationship was consistent across the two sites (binomial test:  $P = 0.0005$ ). Our results therefore agree with previous qualitative assessments in other populations—black-capped chickadee dominance relationships are not site-specific.

### 9.5 Variation in rank acquisition

Analysis of rank histories of known males from our long-term data set provides a revealing picture of the factors associated with change in status (Schubert *et al.* 2006; K. A. Schubert, C. Kraus, D. J. Mennill *et al.* unpublished data). As in willow tits (Lahti *et al.* 1996), rank is a dynamic trait. The majority of mid- and low-status birds increased in rank over consecutive years; birds reaching high rank seldom regressed (Table 9.3; Schubert *et al.* in press). Most birds advancing from low to high rank immediately dominated yearlings (22/29 cases), and some younger or older adult flock-mates (7 cases) (Schubert *et al.* 2006). Not surprisingly, males reaching high rank lived longer, on average ( $3.4 \pm 0.1$  years,  $N = 98$ ) than males who never moved beyond subordinate status ( $1.6 \pm 0.1$  years,  $N = 99$ ,  $P < 0.0001$ ) (Schubert *et al.* in press). Similarly, low-ranked adult males were more

**Table 9.3** Changes in male rank between two consecutive years

Original year	Subsequent year		
	Low	Middle	High
Low (n = 58)	20 (34.5%)	8 (13.8%)	30 (51.7%)
Middle (n = 17)	2 (11.8%)	3 (17.6%)	12 (70.6%)
High (n = 76)	5 (6.6%)	4 (5.3%)	67 (88.2%)

The majority of low- and middle-ranked males increased in rank between years. Few high-ranked males decreased in rank (from Schubert *et al.* in press).

likely to increase in rank than low-ranked juveniles (K. A. Schubert, C. Kraus, D. J. Mennill *et al.*, unpublished data). Rank advancement was not simply a function of survival, however. Of 65 males that eventually attained high rank, 30% achieved dominance in their first year, 35% by the age of 2, and 35% required 3 or more years (Schubert *et al.* 2006). How first-year males achieve dominance is a fascinating question, and may be related to reduced population density in late summer or early autumn (see below). Again, because we have not studied the process of flock formation, our winter rank data do not provide many clues. Smith (1991) reported that first-year birds infrequently achieved high ranks by replacing dead birds. This may explain how some juvenile members in our population attained high rank, since flocks form in October but we assessed dominance in February.

While rank attainment in first-year birds remains a mystery, our data show convincingly that changes in status of adult birds are associated with changes in group composition. Rank increases were often a function of shifting flock membership while former superiors were still alive (16 out of 29 cases) rather than replacement of dead superiors (6 cases) or dominance reversal over a former superior (2 cases); the other 5/29 birds stayed in the same flock but became the second high-ranked male by dominating new juveniles (Schubert *et al.* in press). Changes in flock membership were rare, in that surviving flock-mates—both male and female—frequently reassociated between years (Schubert *et al.* 2006). However, males that remained at low rank tended to reflock with a greater proportion of surviving former flock-mates (64%) than males

rising from low to high rank (39%) (Schubert *et al.* 2006). These results show male chickadees advance in rank predominantly by changing social group rather than out-living their superior flock-mates. Thus, changes in local population density probably have a major influence on whether low-ranking birds can occupy a new home range and attract juveniles as flock-mates. For example, several cases of low-ranking males rising in status by forming new flocks occurred as density declined sharply from 1997 through 1998 and then increased (K. A. Schubert, C. Kraus, D. J. Mennill *et al.* unpublished data; S. Ramsay, personal communication).

## 9.6 Rank, survival, and lifetime reproductive success

Previous shorter-term studies from our group and others (Table 9.1) have documented fitness benefits accrued by high-ranking chickadees in the form of greater over-winter survival (Desrochers *et al.* 1988; Smith 1991), better or larger territories (Desrochers *et al.* 1988; Mennill *et al.* 2004), enhanced success in social and extrapair mate choice (Smith 1988; Otter *et al.* 1994, 1998; Otter and Ratcliffe 1996; Ramsay *et al.* 2000; Bronson *et al.* 2003; Mennill *et al.* 2003b, 2004; Woodcock *et al.* 2005), and greater clutch size, hatching, and fledging success (Otter *et al.* 1999). A primary goal of our long-term analyses was to partition the effects of rank from those of age, and to determine how year effects may influence this relationship.

### 9.6.1 Survival

Schubert (2003) found that adult chickadees at QUBS survived about two winters on average, with 25% of males and 20% of females surviving to a third winter, in general agreement with Smith's (1991) value for average lifespan of 2.5 years. In these analyses, where missing adults were assumed to have died if they were not resighted on the study site, males survived better than females (Cox regression: Wald  $\chi^2 = 4.17$ ,  $N = 436$  females, 427 males,  $P = 0.04$ ). This finding is in agreement with other studies of Parid survival (Desrochers *et al.* 1988; Lens and Dhondt 1993). Interestingly, there was no difference in mean life expectancy of males

that attained high rank in their first year compared to those starting at low rank, nor was there a significant difference in survival to second year for males that achieved high versus low rank as yearlings. The latter result contrasts with Koivula *et al.* (1996) who found social rank predicted survival of juvenile but not adult willow tits.

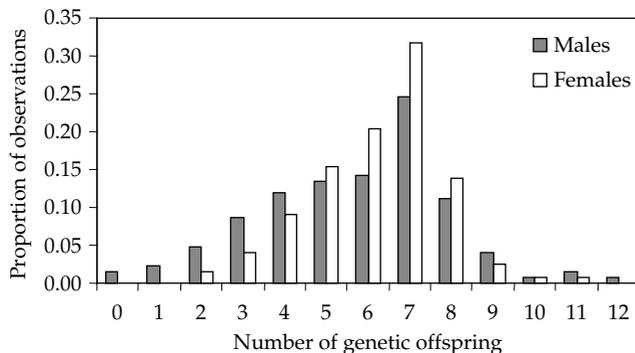
To examine the effects of age and sex on male and female annual survivorship, Schubert (2003) first used nested, generalized linear models (GLZ) to analyze January recapture data from 1994 to 2002. Analyses were performed in MIWiN using a binomial error structure (Goldstein 1995), again assuming that birds that disappeared had died. Our models revealed no significant effects of age (as measured in years), but significant effects of age class (ASY versus SY), and sex, as well as high annual variability. Models of male survivorship which added variables of rank class (e.g. high, mid, low) or rank score (interactions won divided by all interactions) showed rank to be a marginally better predictor of male survival than age ( $P = 0.08$ ). To better untangle the effects of age and rank (here categorized as high or low only), which are tightly correlated, a more targeted analysis applied multistrata, capture–mark–recapture models to resighting data from 1997 to 2002 (K. A. Schubert, C. Kraus, D. J. Mennill *et al.* unpublished data). Population annual survival varied considerably over the 6 years (36–73%), with high-ranked males surviving somewhat better than low-ranked males (annual survival probabilities  $0.56 \pm 0.09$  for high-ranked males vs.  $0.50 \pm 0.08$  for low-ranked males). Moreover, none of the well-supported models

contained an age effect (K. A. Schubert, C. Kraus, D. J. Mennill *et al.* unpublished data). Taken together, these analyses reveal that rank, independent of age, has an influence on annual survival in male chickadees, even in the face of environmental and other variation captured by modeling year effects.

### 9.6.2 Reproductive success

High-ranking males are more attractive social partners to female flock-mates (Schubert 2003), consistent with results from our short-term studies and experiments on female–female competition (Table 9.1). Analysis of 328 pairings from 1994 to 2002 showed that over 70% of high-ranked males but fewer than 40% of low-ranked males paired with adult females. An overwhelming majority (91%) of high-ranked males paired with female flock-mates, whereas only 72% of low-ranked males did ( $P < 0.01$ ); male age was not associated with likelihood of pairing within flock ( $P > 0.6$ ; Schubert 2003). Among pairs of known rank where both survived to breed again, high-ranking males retained social mates somewhat more often (50/58, or 86%) than mid- (3/6, or 50%) or low-ranking males (7/11, or 64%) (K. A. Schubert, unpublished data). Thus high-ranked males benefit from enhanced mate fidelity during the breeding season (Otter *et al.* 1998; Mennill *et al.* 2004).

Figure 9.3 shows annual RRS of males and females in the QUBS population. Average clutch size was  $6.8 \pm 0.1$  eggs ( $N = 185$  clutches), with 92% overall hatching success. Of 240 nests with



**Figure 9.3** Annual realized reproductive success (RRS) of male and female chickadees. Genetic paternity was determined at ca. 6 days after hatching ( $N = 126$  observations for males and 123 for females; from Schubert 2003).

**Table 9.4** Summary of nested models of the influence of male age, female age, and male rank on annual reproductive success

	Nesting ( $i = 264, j = 159$ )		Clutch size ( $i = 128, j = 93$ )		Hatching ( $i = 154, j = 106$ )		RRS ( $i = 80, j = 64$ )		Fledging ( $i = 170, j = 108$ )	
	Coefficient (SE)	Wald stat (P-value)	Coefficient (SE)	Wald stat (P-value)	Coefficient (SE)	Wald stat (P-value)	Coefficient (SE)	Wald stat (P-value)	Coefficient (SE)	Wald stat (P-value)
Intercept	0.59 (0.24)		-0.48 (0.18)		-0.40 (0.17)		-0.61 (0.23)		1.24 (1.16)	
Male age	1.16 (0.45)	6.62 (0.01)	0.29 (0.21)	1.96 (0.16)	0.42 (0.20)	4.62 (0.03)	0.35 (0.26)	1.84 (0.17)	0.46 (0.47)	0.96 (0.33)
Female age	NA	NA	0.27 (0.18)	2.20 (0.14)	0.05 (0.17)	0.07 (0.79)	0.17 (0.23)	0.57 (0.45)	0.02 (0.42)	0.00 (0.97)
Male rank (H)	2.12 (0.67)	9.94 (<0.01)	0.18 (0.21)	0.76 (0.38)	0.13 (0.20)	0.40 (0.53)	0.47 (0.27)	3.17 (0.08)	0.06 (0.46)	0.02 (0.90)
Male rank (M)	0.63 (0.54)	1.34 (0.25)	0.04 (0.28)	0.02 (0.89)	-0.21 (0.27)	0.60 (0.44)	-0.12 (0.33)	0.14 (0.71)	-1.07 (0.61)	3.07 (0.08)

Model coefficients are given with standard errors. Wald statistics are accompanied by significance values at 1 d.f. Sample sizes  $i$  and  $j$  denote the number of observations and number of individual male birds, respectively. *Clutch size*, *hatching*, and *RRS* (number of genetic offspring at day six post-hatch) are standardized within year as  $(x - x_{\text{mean}})/\text{SD}$ ; models of *nesting* and *fledging* success use binomial response data. The full *fledging* model included additional year effects not presented here. *Male age* and *female age* represent the effects of adult vs. juvenile age category on breeding success. *Male rank* variables represent contrasts of high- and mid-ranked males against low-ranked males (modified from Schubert 2003).

known outcomes, 56% fledged at least one offspring. Successful pairs fledged an average of  $6.3 \pm 0.1$  young; 29.8% of broods contained extra-pair young ( $N = 131$ ), with an average of 11% extra-pair young per brood ( $N = 73$ ), remarkably consistent with our initial estimates of EPY based on a much smaller sample of nests (Otter *et al.* 1994). Annual reproductive success was lower in males than females: only 87% of males, but 93% of females, paired and attempted to breed ( $P = 0.03$ ). The standardized variance in annual RRS was larger in males (0.16) than females (0.07), consistent with moderate levels of extra-pair paternity.

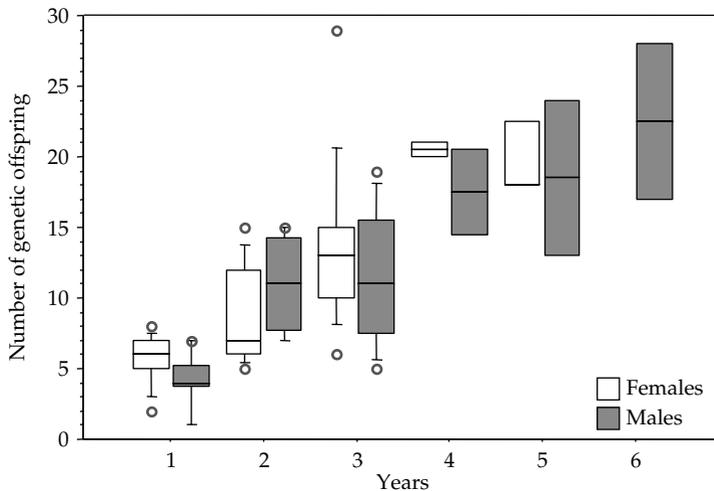
Table 9.4 summarizes the results of nested GLZ analyses of the effects of male and female age and male rank on annual reproductive success (Schubert 2003). Both male age and rank influenced whether a male paired with a female and attempted any nesting ( $P < 0.02$ ). However, compared to age, male rank may be a stronger predictor of male RRS ( $P = 0.08$ ). Surprisingly rank was not associated with clutch size, hatching, or fledging success in this model, in contrast to the results of Otter *et al.* (1999), which was based on 2 years' breeding data, including a year of severe nest predation. Thus the benefits of rank probably vary from year to year (see Chapter 17 for evidence of annual variation in effects of habitat quality).

Lifetime reproductive success of both males and females was highly variable and heavily influenced

by lifespan ( $P_s < 0.0001$ ) (Fig. 9.4). To test the effect of male rank over time on LRS, we calculated the sum of all ranks held by a male, where 1 = low, 2 = mid, and 3 = high rank in each year. Average lifetime rank (the sum of ranks held divided by lifespan) significantly predicted whether a male attempted to reproduce ( $P < 0.01$ ). However rank sum/lifespan did not predict LRS among the subset of males that succeeded in reproducing ( $P = 0.2$ ). In other words, males that lived longer and reached higher rank sooner had greater fitness, but this was a function of whether birds reproduced at all, rather than fine-scale differences between individuals.

## 9.7 Future research

Male black-capped chickadees at QUBS vary in their ability to dominate competitors, and high social rank enhances both annual survival and reproduction, leading in turn to increased LRS. Although our study was not initiated in 1992 with a long-term design, and the data set is admittedly limited, the results suggest several profitable avenues for further research. One obvious question concerns the source(s) of individual variability in signaling behavior associated with rank, including the role of experience in modulating individuals' responses to competitors and potential mates. Careful measurement of ontogenetic changes in plumage, vocalizations, and dominance behavior,



**Figure 9.4** The relationship between lifespan and lifetime reproductive success (LRS). LRS estimates are based on the total number of genetic offspring attributed to 51 male and 56 female chickadees and do not include birds that never bred (from Schubert 2003).

coupled with their associated effects on male and female receivers, are required.

A second, related question concerns the factors that contribute to individual variation in first-year rank. Our analyses point to male rank history as a key predictor of fitness, thus it would be useful to identify the individual attributes and ecological circumstances that combine to permit some males to achieve high rank in their first year. For example, short-term aviary experiments using juveniles captured in late summer could measure behavioral predictors of dominance (e.g. Verbeek *et al.* 1999). Temporary removal of dominant adults from natural flocks might also provide useful opportunities to observe flock fission and reassembly, as suggested by Smith (1991). Ideally, such experiments should be combined with detailed information on both temporal and geographic variation in population density, to determine whether our findings extend to other parts of the species' range. Ironically, this critically important flock formation period remains the least-studied part of the chickadee annual cycle.

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