Variation in social rank acquisition influences lifetime reproductive success in black-capped chickadees

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Dominance relationships structure many animal societies, yet the process of rank attainment is poorly understood. We investigated acquisition of social dominance in winter flocks and its fitness consequences in male black-capped chickadees *(Poecile atricapillus)* over a 10-year period. Age was the best predictor of rank, and paired comparisons showed high-ranked males to be older than their low-ranked flock-mates. When controlling for age, morphological variables did not predict male social rank, but high-ranked males were heavier, had lower fat scores and were in leaner condition than low-ranked males. Males that survived between years tended to increase in rank over time; however, the rate of rank advancement varied individually. Rank reversals between familiar contestants were rare, and changes in male social rank were associated with changes in flock membership. Average lifetime reproductive success (LRS) of males and females was variable and best predicted by lifespan. Male rank history also influenced realized reproductive success. Birds with higher average rank over their lifespan were more likely to reproduce successfully. However, among successful birds, average rank did not significantly predict LRS. Thus, birds that lived longer and attained high social rank earlier had higher fitness, but this effect was not manifested as fine-scale differences among successful individuals. Taken together, these findings demonstrate the importance of social factors influencing individual fitness. © 2007 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2007, **90**, 85–95.

ADDITIONAL KEYWORDS: dominance – flock fidelity – individual history.

INTRODUCTION

Dominance relationships are salient features of many animal societies (Wilson, 1975; Clutton-Brock, Guinness & Albon, 1982; Silk, 1987; Festa-Bianchet, 1991; Creel & Macdonald, 1995). Individuals with high social status derive a variety of rank-related benefits, including preferential access to resources (Ekman, 1987; Desrochers, 1989), enhanced survival (Ekman & Askenmo, 1984; Koivula, Orell & Rytkonen, 1996), and enhanced reproductive success (Ellis, 1995; Otter

et al., 1998; Mennill & Ratcliffe, 2004). Despite our understanding of the benefits of social rank, the process of rank acquisition remains poorly understood, and the consequences of variation in rank acquisition for individual fitness have received little attention.

Social dominance in birds generally relates to age or prior residence (prior residence; Piper, 1998) rather than differences in body size (but see Ketterson, 1979; Hogstad, 1987b; Ramsay & Ratcliffe, 2003). Prior residency influences rank relationships between unfamiliar competitors when other factors are equal (Krebs, 1982; Sandall & Smith, 1991; Dearborn & Wiley, 1993; Koivula et al., 1993), and may even predict dominance between individuals with prior asymmetries in experience (Cristol, Nolan & Ketterson, 1990). Reversals of

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dominance between familiar contestants usually are rare (Archawaranon, Dove & Wiley, 1991; Wiley *et al*., 1999; but see also Schjelderup-Ebbe, 1922; Caldow & Goss-Custard, 1996). Thus, rank shifts typically occur when a superior dies (Wiley & Rabenold, 1984), a subordinate emigrates to a new area (Hogstad, 1999), or naïve individuals join a flock. Low-ranking individuals may be 'hopeful dominants' who tolerate temporary subordination in anticipation of future benefits (West-Eberhard, 1975; Wiley & Rabenold, 1984).

Lifetime reproductive success (LRS) is one of the most tractable measures of fitness because it allows for the comparison of the overall genetic contribution of individuals with different lifespans or reproductive strategies (Newton, 1989). Reproductive lifespan is the most important predictor of LRS (Clutton-Brock, 1988; Newton, 1989); however, few studies have explicitly investigated the relationship between key phenotypic traits, such as social rank, and LRS.

BLACK-CAPPED CHICKADEES

Black-capped chickadees (*Poecile atricapillus*) spend the winter in flocks of 3–12 birds, typically consisting of one or more adult pairs plus a number of yearlings (Smith, 1991). Flocks have stable membership over a given season and are characterized by linear dominance hierarchies where males dominate females, and mature birds typically dominate yearlings (Smith, 1991). Male rank correlates with age, although the process of rank acquisition has not been studied. The correlates of female rank are poorly understood (Smith, 1991; but see also Ramsay & Ratcliffe, 2003) because females interact with each other less overtly than males do.

High-ranked males benefit from their status, both in winter and during the breeding season. They have greater over-winter survival than low-ranking males (Desrochers, Hannon & Nordin, 1988) resulting from preferential access to food (Ficken, Weise & Popp, 1990), roosting sites, and foraging sites (Desrochers, 1989), as well as reduced predation risk (Zanette & Ratcliffe, 1994). Both members of high-ranked pairs are more likely to survive to the breeding season (Smith, 1991).

High-ranking males are more likely to obtain breeding territories (Desrochers *et al*., 1988), and their territories are larger than those of low-ranking males (Mennill *et al*., 2004). The mates of high-ranking males have larger clutches with increased hatching and fledging success (Otter, Ramsay & Ratcliffe, 1999). Although high-ranking males do not provision their nests more than low-ranking males, their mates have longer incubation bouts (Otter *et al*., 1999). An average of 31.3% of chickadee broods contain extra-pair young (EPY), and 11.85% of all offspring are extra-pair (Otter *et al*., 1998; Mennill *et al*., 2004). The broods of high-ranking males contain significantly fewer EPY than the broods of low-ranking males (Mennill *et al*., 2004). Females seek extra-pair copulations from males that are socially dominant to their partners, which consequently enhances the realized reproductive success (RRS) of high-ranked males (Otter *et al*., 1998; Mennill *et al*., 2004). High-ranking males are also preferentially chosen as social mates by divorcing females (Otter & Ratcliffe, 1996; Ramsay *et al*., 2000). Thus, social rank provides a likely mechanism for sexually selected variation in male reproductive success.

The present study aimed to describe the process of rank acquisition by characterizing changes in rank among individuals. We evaluated LRS for males whose dominance status was monitored over a 10-year period. We examined the correlates of rank acquisition and modelled the effects of this process on LRS.

MATERIAL AND METHODS

STUDY AREA AND POPULATION

We studied black-capped chickadees in a 2-km² study site at Queen's University Biological Station, near Chaffeys Lock, Ontario, Canada (44°34′N, 76°19′W), from 1992 to 2002. All data prior to the 2002 field season were collected in the context of other studies, with breeding data collected beginning in 1992 and dominance data collected from 1994 onwards (see below). Data collection methods were similar across years. Because chickadees are highly philopatric during adulthood (K. A. Schubert, pers. observ., Smith, 1991), we assumed adult disappearances to be due to mortality.

WINTER FIELD METHODS

From January until March of 1992–2002, birds were attracted to feeding stations baited with sunflower seeds. Using Potter traps, we captured between 86 and 198 individuals per year (mean ± SEM = 146.8 ± 12.5). Each individual was banded with a Canadian Wildlife Service number band and one to three plastic colour bands in unique combinations.

We measured mass, tarsus, wing, tail, and fat score, and drew approximately 10–80 µL of blood for molecular analyses from captured individuals. We calculated a condition index as the ratio of body mass to tarsus length for each individual. We used rectrix shape and wear to assign birds to second-year (SY) or after-second-year (ASY) age classes (Pyle *et al*., 1987). Birds first banded as adults were conservatively assumed to be in their second year of life. The sexes of birds were determined using a discriminant function including body mass, wing, and tail lengths (Desro-

chers, 1989). Sexes were later confirmed from breeding behaviour.

A total of 155 flocks (identified as groups of birds consistently observed together and which associated together in the absence of other birds) were monitored from 1994 to 2002 (mean = 17.2 ± 2.1 flocks year^{-1}; flock memberships were not recorded prior to 1994). Dominance interactions were quantified by scoring the outcomes of the following competitive interactions at winter feeding stations: supplants, chases, resistance to supplants, displays of submissive postures, and feeding while an opponent waited to approach (Ficken *et al*., 1990; Otter *et al*., 1998).

RANK DEFINITIONS

Relative ranks of males within flocks were based on a total of 2659 interactions, with a range of 1–24 interactions per dyad (mean = 2.8 ± 0.1). Because interactions between females are less overt and frequent than interactions between males, we limited our investigation to dominance in males. Dyadic interactions were tabulated in matrices ordered as linear hierarchies (de Vries, 1998) using MatMan software (Noldus Information Technology). Males were assigned to nominal within-flock classes of 'high', 'middle', and 'low' following Mennill *et al*. (2004), where high-ranking males were the top male in flocks with two or three males, or the top two in flocks with four or five males; mid-ranking males were the middle individuals in flocks of three or five males; and low-ranking males were the bottom male in flocks with two or three males or the bottom two in flocks with four or five males.

SPRING FIELD METHODS

Breeding data were collected from 1992 to 2002, with a total of 536 pairings observed (mean = 60 ± 8.2 pairs year^{-1}, including mate-switches within years). Many individuals reproduced in several years and, accordingly, breeding season data include observations for a total of 294 individual males and 282 females. Pairs were monitored beginning at flock break-up (typically mid-March to late April) to determine territory boundaries and nest-sites. Pairing status was assessed based on affiliative behaviours, including cavity excavation, nuptial feeding, copulation, mate guarding, and territorial defense (Otter & Ratcliffe, 1996). Disappearances or changes in pairing status were recorded. Birds remaining unpaired throughout the breeding season were assumed not to have reproduced (see section below: 'Structure of long-term data'). Nests were identified from excavation behaviour and confirmed by the lining of cavities, egg-laying, and/or incubation. The onset of egg-laying was apparent when females gave a sex-specific vocalization made at the onset of fertility (the 'broken-dee' call; Smith, 1991; Mennill *et al*., 2004). At approximately day 6 posthatch, 10–50 µL of blood were collected from the tarsal vein of nestlings for paternity analysis.

MEASURES OF GENETIC SUCCESS

Details of paternity assignments are provided in Otter *et al*. (1998) and Mennill *et al*. (2004). Measures of genetic reproductive success included only pairs for which nests were sampled from 1994 to 2001; survival of nestlings to day 6 was a precondition of measuring RRS. Male RRS was calculated as the total number of within-pair plus extra-pair young. Female RRS equalled the total number of offspring within her nest because egg dumping was extremely rare (Otter *et al*., 1998; Mennill *et al*., 2004). From 1999 to 2001, several males were subject to experimental playback treatments that affected RRS (Mennill, Ratcliffe & Boag, 2002; Mennill, Boag & Ratcliffe, 2003). We excluded data from all males receiving manipulative but not control playback treatments (playback treatments were balanced with regard to male rank such that exclusion of experimentally manipulated birds did not bias our dataset).

STRUCTURE OF LONG-TERM DATA

Our LRS analyses were based on breeding data of two types: (1) whether birds had paired and attempted reproduction and (2) RRS for birds from nests where hatched young were sampled. Previous research in this population has demonstrated that unpaired males do not father EPY (Otter *et al*., 1998; Mennill *et al*., 2004).

Individual breeding data were not available in all years, partly due to exclusion of RRS data (see above). Thus, we analysed LRS data for a subset of birds that would be representative of the true population. Our goal was first to create a global LRS estimate for each bird. We did this by adding all years of RRS, plus all years in which birds were confirmed nonbreeders (RRS = 0). Using the number of years with known breeding success for each bird (B_{data}), we measured data completeness as:

$$\% gaps = \frac{B_{data}}{B_{alive}} \times 100$$

where B_{alive} was the number of years the bird was alive and could have reproduced. We could not include data for birds that did pair and attempt reproduction, but for which genetic success was missing or excluded. Consequently, individual LRS values are underestimates but demonstrate the relationship between LRS, rank acquisition and lifespan.

Individual breeding records were also used to estimate population-wide LRS. We first calculated the mean age-specific reproductive success for males and females, as measured by the number of genetic offspring (Table 1). Again, we assigned unpaired birds a reproductive success of 0 for that year; records for paired birds with an unknown number of offspring were omitted. Because only a few breeding birds were older than 5 years, we substituted values at age 5 years for the success rates of older birds. We combined these data with the total number of breeding seasons that each bird in the population ($N = 427$ males, 436 females) was alive, similar to the total lifespan. From this, we summed average reproductive success across breeding lifespan to estimate LRS across the population. For each record:

$$LRS = \sum_{i=1}^{n} B_i$$

where i represents age, B_i is the mean sex-specific reproductive success at age i, and n is the age in years when the bird was last observed during a breeding season. We calculated mean LRS for males and females separately.

Estimates of mean individual LRS were lower than mean population-level LRS. Therefore, we chose to analyse the subset of data with the highest mean LRS for each of males and females in analyses of rank and longevity vs. LRS. Our models include birds where %gaps < 50% for individual breeding data (mean LRS: males, 6.4 ± 0.8, $N = 73$; females, 8.4 ± 0.8, $N = 72$). We followed the same approach for male rank history: birds with %gaps > 50% were omitted from analysis. To test the effect of rank over time on LRS, we calculated the sum of all ranks held by each male (rank sum). We assigned a value of 1 for a low rank, 2 for a middle rank, and 3 for a high rank in each year. In models of LRS, we used rank sum/lifespan as a predictor variable, which is equivalent to average rank over an individual's lifetime. We did this instead of taking the residuals of the rank sum/lifespan relationship because we were unable to produce a model with normally distributed residuals.

STATISTICAL ANALYSIS

We present data as mean ± SEM. Standardized variances are denoted as σ^2/x^2_{mean}. All tests are two-tailed. Sample sizes vary according to the question and are indicated throughout.

Some analyses dealt with data containing multiple observations for the same individuals or flocks (see sections below: 'Correlates of rank' and 'Changes in rank'). We avoided pseudoreplication by taking subsets of data that included only unique entries. For example, to compare body size of high- and low-ranked

Table 1. Age-specific annual reproductive success data for male and female chickadees, as measured by the number of genetic offspring

Variable	Breeding season							
	1	2	3	4	5	6	7	8
Male RRS	5.1 ± 0.3 (50)	6.0 ± 0.4 (41)	5.6 ± 0.4 (27)	6.4 ± 0.4 (23)	6.4 ± 0.8 (9)	6.3 ± 1.5 (3)	NA	8.0 ± 0.0 (1)
Female RRS	5.9 ± 0.2 (47)	6.3 ± 0.3 (52)	6.6 ± 0.4 (24)	6.4 ± 0.4 (11)	6.5 ± 0.5 (2)	6.5 ± 1.5 (2)	6.0 ± 0.0 (1)	NA

Data are means ± standard error, with samples sizes given in parentheses. These data were used in creating population-level estimates of lifetime reproductive success (see Material and methods) by summing average reproductive success rates for each breeding season a bird was alive. NA, not applicable. RRS, realized reproductive success; NA, not applicable.

flock-mates, we created multiple subsets of data containing a given high-low dyad only once and each flock no more than once. We chose data at random and without replacement using Visual Basic macros for Microsoft Excel (Microsoft Corporation, Redmond, WA, USA). We calculated a test statistic for each subset of the data (1000 per analysis), and then used the average of this statistic to evaluate significance at $\alpha = 0.05$ (Morbey *et al.*, 1999).

We analysed the influence of male age and rank on annual reproductive success using multilevel generalized linear models (ML-GLZ) in MlwiN 1.1 (Multilevel Models Project, Institute of Education, University of London, 2000). Here, our goal was to expand on the findings in Otter *et al.* (1999) using a long-term dataset. These models explicitly account for variance occurring at multiple levels of organization; for example within and among individuals. Some individuals bred in several years, so we nested each observation (level one, i) within individual identity (level two, j). Each level was identified as a random effect, and predictor variables were fitted as fixed effects. Estimation was performed with second-order penalized quasi-likelihood and the restricted, iterative generalized least squares estimation procedure (Rasbash *et al.*, 2000). We modelled pairing success with a binomial distribution and a logit-link function; RRS for successful birds (count data) was modelled with a Poisson distribution and a log-link function. Significance was assessed from the Wald statistic (W), which follows a χ^2 distribution. Models including interactions between age and rank did not converge and are not presented here.

Finally, we explored the relationship between life expectancy and rank history using generalized linear models (GLZ) in Statistica 6.1 (StatSoft, Inc. 2002). As above, we used a binomial distribution to test whether birds ever bred successfully, and a Poisson distribution to model lifetime RRS for successful individuals (LRS > 0). Here, we report Wald statistics that have been divided by $\sqrt{(\text{deviance/d.f.})}$ to correct for overdispersion. Parameter estimates for GLZ and ML-GLZ are designated by β in the text.

RESULTS

CORRELATES OF RANK

Dyadic comparisons of the highest- and lowest-ranked males within flocks revealed that high-ranking males were significantly older than low-ranking males (high-ranked males = 3.4 ± 0.2 years, low-ranked males = 1.6 ± 0.1 years; $t_{132} = 9.3$, $P < 0.0001$). The relationship between age and rank was also strong outside the dyadic context. On average, high-ranking males were aged 3.2 ± 0.1 years ($N = 168$) whereas low-ranking males were aged 1.5 ± 0.1 years ($N = 168$; Fig. 1).
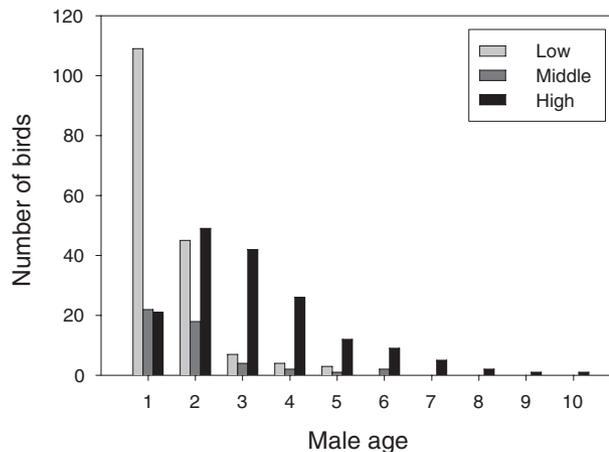
Figure 1. The relationship between male age and rank. Average ages were 1.5 ± 0.1 years ($N = 168$ observations) for low-ranked males, 1.9 ± 0.2 years ($N = 49$ observations) for middle-ranked males, and 3.2 ± 0.1 years ($N = 168$ observations) for high-ranked males. Individuals are included for every year in which their rank was known.

In paired comparisons of the highest- and lowest-ranked male in each flock, we found that high-ranking males had longer wings and tarsi than low-ranking males (wing: high = 66.6 ± 0.2 mm, low = 66.2 ± 0.1 mm, $t_{119} = 1.9$, $P = 0.03$; tarsus: high = 15.67 ± 0.11 mm, low = 15.18 ± 0.08 mm, $t_{108} = 5.11$, $P < 0.0001$). High-ranking males did not have longer tails or weigh more than low-ranking males (tail: high = 62.7 ± 0.3 mm, low = 62.3 ± 0.2 mm, $t_{114} = 1.1$, $P = 0.14$; weight: high = 11.87 ± 0.05 g, low = 11.80 ± 0.05 g, $t_{116} = 0.68$, $P = 0.25$). However, high-ranked males were leaner (fat score: high = 2.2 ± 0.1, low = 2.4 ± 0.1, $t_{79} = -2.2$, $P = 0.02$; mass/tarsus: high = 0.76 ± 0.01, low = 0.78 ± 0.00, $t_{106} = -4.05$, $P < 0.0001$).

Differences in wing and tarsus lengths reflected age asymmetries. Comparing age-matched pairs of high- and low-ranked flock-mates revealed no differences in wing, tail, or tarsus length (wing: high = 67.0 ± 0.4 mm, low = 67.1 ± 0.4 mm, $t_{21} = -0.2$, $P = 0.42$; tail: high = 63.1 ± 0.6 mm, low = 63.0 ± 0.4 mm, $t_{21} = 0.2$, $P = 0.42$; tarsus: high = 15.07 ± 0.19 mm, low = 15.08 ± 0.20 mm, $t_{21} = -0.05$, $P = 0.48$). However, in this comparison, low-ranked birds were heavier and had greater fat and condition scores (weight: high = 11.63 ± 0.10 g, low = 11.95 ± 0.11 g, $t_{21} = -2.37$, $P = 0.01$; fat score: high = 1.9 ± 0.2, low = 2.5 ± 0.2, $t_{19} = -2.4$, $P = 0.01$; mass/tarsus: high = 0.77 ± 0.01, low = 0.80 ± 0.01, $t_{21} = -2.17$, $P = 0.02$).

FLOCK MEMBERSHIP BETWEEN YEARS

Former flock-mates often re-associated from one winter to the next. On average, 2.7 ± 0.1 of the birds in a

flock survived to the next winter (mean flock size = 5.4 ± 0.1 individuals, $N = 155$ flocks). Surviving birds from a given flock were members of 1.4 ± 0.1 new flocks on average ($N = 95$ flocks for which subsequent flock memberships were known); the ratio of new flocks to surviving birds was 0.63 ± 0.03 (for the 89 flocks with ≥ 1 survivor). Considering flocks with at least two survivors, we counted how often there were fewer new flocks than surviving members. This was true in 58 of 70 cases (binomial test, $\chi^2_{69} = 32.9$, $P < 0.0001$); therefore, at least two birds from a flock would likely flock together in the next winter.

CHANGES IN RANK

Individuals increased in rank over successive winters and seldom lost high status once they attained it (Table 2); only nine of 76 dominant males fell in rank between years. Males reaching high rank lived longer than males whose greatest rank was low (high: 3.4 ± 0.1 years, $N = 98$ birds; low: 1.6 ± 0.1 years, $N = 99$ birds; $t_{2,197} = 9.3$, $P < 0.0001$). There were 200 males with known ranks in their last year of life. Of these, 42.0% attained high rank, 13.0% attained middle rank, and 45.0% remained at low rank throughout their lives. Only 24.6% of 118 males we first observed at low- and middle-rank eventually reached high rank. Among birds eventually attaining high rank, the rate of increase was variable. Most males to reach high rank had done so by age 2 years (mean age = 2.0 ± 0.1, $N = 61$ males); however, 28% did not do so until aged 3 years or older (Fig. 2).

In most cases where a male advanced from low to high rank (23/29), at least one of his former superiors was still living. Only two of these 23 rank changes resulted from reversals in dominance status between flock-mates. Five males re-flocked with at least one former superior but advanced in rank when joined by new, low-ranked birds (all juveniles). Sixteen males with surviving superiors advanced in rank by switching flocks. Most birds advancing from low to high rank immediately dominated yearlings (22 of 29 cases).

The proportion of surviving flock-mates with which an individual re-associated was greater for males staying at low-rank (LL males) than males increasing from low to high rank (LH males) (overall: $t_{2,43} = 2.2$, $P = 0.04$; male flock-mates: $t_{2,36} = 2.3$, $P = 0.03$; female flock-mates: $t_{2,39} = 2.0$, $P = 0.05$; Table 3). LL males were more likely to re-flock with one or more formerly dominant flock-mates (superiors) than LH males ($\chi^2_{1,45} = 6.0$, $P = 0.02$). LL males re-associated with more surviving superiors than LH males. They did not initially have more superiors, nor did more of their superiors survive (N: HH = 67, LH = 29, LL = 19; number of superiors: HH = 0.2, LH = 1.8, LL = 1.7, $t_{2,44} = -0.8$, $P = 0.46$; superiors surviving: HH = 0.4,
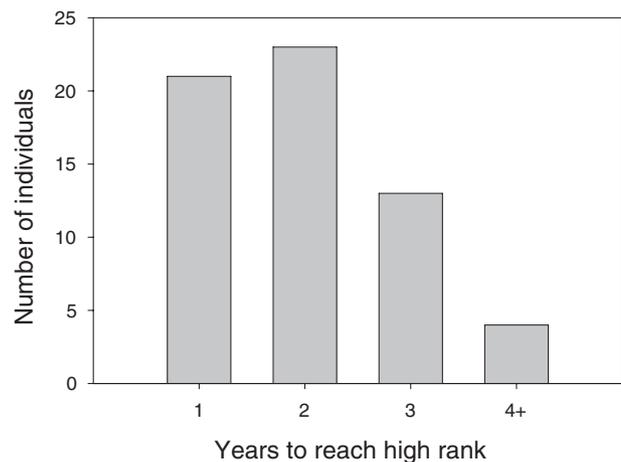
Figure 2. The age by which males reached high rank. The majority of males that eventually reached high-rank had done so by their second winter, although some males only attained high rank later in life. All males ($N = 61$) who achieved high rank are included, with the exception of those with missing rank data in the year immediately preceding their first year at high rank.

Table 3. The proportion of surviving flock-mates with which males associated in consecutive years

Male type	Proportion of surviving flock-mates		
	Male	Female	Overall
HH ($N = 67$)	0.45	0.70	0.57
LH ($N = 30$)	0.28	0.49	0.39
LL ($N = 20$)	0.62	0.75	0.64

Males remaining at low-rank between two different years (LL males) re-flocked with a significantly greater proportion of surviving flock-mates than males rising to high rank (LH males, see text for statistical comparisons). Males beginning and remaining at high rank (HH males) are shown for reference. Sample sizes are given in parentheses.

Table 2. Male rank between consecutive years

First year	Following year		
	Low	Middle	High
Low ($N = 55$)	19 (34.5%)	7 (12.7%)	29 (52.7%)
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.

LH = 1.0, LL = 1.2, $t_{2,44}$ = 1.0, P = 0.33; superiors reflocking: HH = 0.2, LH = 0.2, LL = 0.8, $t_{2,44}$ = 3.0, P = 0.005). In short, males that stayed at low-rank remained in flocks with relatively stable membership, whereas rank advancement was associated with changes in flock affiliation.

ANNUAL AND LIFETIME REPRODUCTIVE SUCCESS

Male rank was associated with enhanced annual reproductive success. A male's age category and rank significantly influenced whether he paired with a nesting female (Table 4), and male rank was the single best predictor of annual RRS (Table 5). When incorporating male age, female age and male rank, the effect of rank on male RRS was nonsignificant (P = 0.08). Likely because rank and age are tightly related, including both factors generated a model in which no single factor was significant. A simplified model with rank alone showed a significant effect of rank on annual RRS (Poisson ML-GLZ; fixed effects: W_2 = 14.9, P = 0.0006; male rank [high]: $\beta \pm$ SEM = 0.8 ± 0.2, W_1 = 11.6, P = 0.0007; male rank [middle]: $\beta \pm$ SEM = 0.0 ± 0.3, W_1 = 0.0, P = 0.95; random effects: i = 82,

σ^2_i = 0.5 ± 0.2, W_1 = 9.2, P = 0.002; j = 65, σ^2_j = 0.4 ± 0.2, W_1 = 5.0, P = 0.02).

LRS estimated from population-level annual fecundity and breeding lifespan was highly variable. Average male LRS was 6.9 ± 0.4 young (maximum = 58.5 young, N = 427 males, σ^2/x^2_{mean} = 1.6; Fig. 3), or 9.3 ± 0.5 offspring (N = 319 males, σ^2/x^2_{mean} = 1.0) after excluding males with zero LRS. Average female success was 6.8 ± 0.4 young (maximum = 42.4 young, N = 436 females, σ^2/x^2_{mean} = 1.4; Fig. 3), or 9.6 ± 0.5 young (N = 307 females, σ^2/x^2_{mean} = 0.7) for females with LRS ≥ 1.

Lifespan significantly predicted whether males produced any offspring (binomial GLZ, 0 = no, 1 = yes; males: deviation = 77.0, $\beta \pm$ SD = 1.2 ± 0.5, $W_{2,71}$ = 7.5, P = 0.006; females: deviation = 59.7, $\beta \pm$ SD = 1.6 ± 0.5, $W_{2,70}$ = 10.5, P = 0.001). Lifespan also predicted LRS for the subset of successful individuals with ≥1 young (Poisson GLZ; males: deviation = 79.8, $\beta \pm$ SD = 0.3 ± 0.0, $W_{2,47}$ = 86.5, P < 0.0001; females: deviation = 74.3, $\beta \pm$ SD = 0.3 ± 0.0, $W_{2,54}$ = 83.9, P < 0.0001).

When controlling for lifespan, a male's rank sum significantly predicted whether he had LRS > 0 (binomial GLZ, 0 = no, 1 = yes; deviation = 44.4, $\beta \pm$ SD =

Table 4. Nested model * of the influence of male age class and rank on whether a male paired with a female that attempted to nest (binomial ML-GLZ, 1 = yes, 0 = no; fixed effects: W_3 = 27.0, P < 0.0001)

Variable	Coefficient	SEM	Wald statistic	d.f.	P-value
Male age class	1.2	0.5	6.6	1	0.01
Male rank (high)	2.1	0.7	9.9	1	< 0.01
Male rank (middle)	0.6	0.5	1.3	1	0.25

*Random effects: i = 264, σ^2_i = 1.0 ± 0.0, W_1 = not applicable, P < 0.0001; j = 159, σ^2_j = 0.0 ± 0.0, W_1 = not applicable, P = 1.0. Nesting level one (i) represents observation number; level two (j) represents individual male identity. Male age class gives success of adult birds in relation to yearlings. Male rank gives success of high- and middle-ranked birds compared to low-ranked birds.
SEM, standard error of the mean; d.f., degrees of freedom.

Table 5. Nested model * of factors influencing male annual realized reproductive success (within- and extra-pair young observed at sampling, approximately day 6 posthatch, standardized within year as [$x - x_{mean}$]/SD)

Variable	Coefficient	SEM	Wald statistic	d.f.	P-value
Male age class	0.4	0.3	1.8	1	0.17
Female age class	0.2	0.2	0.6	1	0.45
Male rank (high)	0.5	0.3	3.2	1	0.08
Male rank (middle)	−0.1	0.3	0.1	1	0.71

*Random effects: i = 80, σ^2_i = 0.6 ± 0.2, W1 = 9.2, P < 0.0001; j = 64, σ^2_j = 0.3 ± 0.2, W_1 = 2.6, P = 0.11.
Model incorporates male age class, female age class and male rank (Poisson ML-GLZ; fixed effects: W4 = 15.10, P = 0.005). Nesting level one (i) represents observation number; level two (j) represents individual male identity. Male and female age class each give the RRS of adult birds in relation to yearlings. Male rank gives success of high- and middle-ranked pairs compared to low-ranked pairs.
SD, standard deviation; SEM, standard error of the mean; d.f., degrees of freedom.
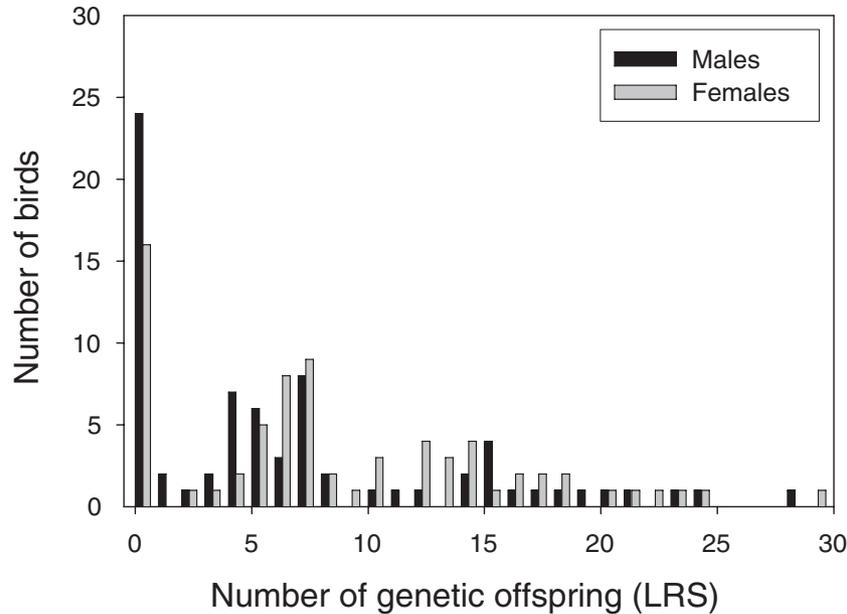
Figure 3. Lifetime realized reproductive success for males ($N = 73$ individuals) and females ($N = 72$ individuals). The number of genetic offspring is based on sampling, approximately day 6 posthatch. Birds that never bred ($N = 24$ males, 16 females) have values of zero. Data represent observed values for birds with fewer than 50% missing observations (see text).

3.0 ± 1.3, $W_{2,46} = 7.2$, $P = 0.007$). However, rank sum/ lifespan did not predict LRS among the subset of successfully reproducing males (Poisson GLZ: deviation = 142.2, $\beta \pm SD = 0.2 \pm 0.2$, $W_{2,29} = 1.6$, $P = 0.20$). Thus, males that lived longer and reached higher rank sooner had a higher probability of reproducing. However, rank effects did not explain fine-scale differences among successful individuals.

DISCUSSION

We explored variation in rank acquisition and the effects on fitness of individual black-capped chickadees. Over 10 years, most males recruited as low-ranking flock members but surviving males advanced in rank between years. Thus, low-ranking birds may be 'hopeful dominants' standing to gain long-term benefits after a period of early subordination (West-Eberhard, 1975; Ekman & Askenmo, 1984; Lahti *et al.*, 1996). Our analyses show that low rank is a temporary state for most males. Although males tend to increase in rank as they age, we found individual variation in both life expectancy and the rate of rank acquisition. Increases in status likely represent an interaction between individual attributes and social opportunities.

ASYMMETRIES UNDERLYING RANK RELATIONSHIPS
The results of the present study corroborate previous evidence that winter rank is strongly dependent on

age in free-living black-capped chickadees (Glase, 1973). We initially found dominant males to be larger than subordinates; however, when controlling for age, these differences disappeared. Other studies on Parids have provided little evidence for effects of size on dominance (Glase, 1973), although Hogstad (1987b) found that dominant willow tits (*Parus montanus*) had longer wings.

In contrast to size, we found rank-related differences in weight, fat score and condition (mass/tarsus). Low-ranking males in this population were heavier and carried more fat than their high-ranked flockmates. This result agrees with literature on winter fattening strategies, which suggests that low-ranking birds must carry more fat in resource-limited environments (Clark & Ekman, 1995; Gosler, 1996; Hake, 1996; Pravosudov *et al.*, 1999). Dominant individuals with certain access to food may not depend on fat reserves. However, rank differences in energy demands may also explain the relationship between rank and fat storage. High metabolic rate may be a cost of dominance (Røskaft *et al.*, 1986; Hogstad, 1987a; but see also Vézina & Thomas, 2000).

RANK AS A DYNAMIC PHENOTYPIC TRAIT
We found that individual rank changed over time, with the majority of surviving males increasing in rank over their lifespan. These results agree with the few other avian studies on dynamic changes in individual social status (Piper & Wiley, 1989; Caldow &

Goss-Custard, 1996; Lahti *et al.*, 1996). Site seniority may be important for rank advancement; however, survival alone does not ensure that an individual will increase in rank. We found that flock-mates tended to re-associate between years. Rank advancement occurred primarily through changes in flock membership, which may accompany changes in location. The present study is the first to quantify flock associations between years in chickadees.

We suggest three possible explanations for the individual variability in rank acquisition we observed. First, there may be yet-undetected benefits for individuals remaining at low rank between years. We found no evidence that birds staying at low rank benefit through the retention of pair bonds (K. A. Schubert, unpubl. data). However, they may benefit in other ways, perhaps through survivorship or by inheriting breeding territories in the following year. Second, males advanced in rank when their superiors died or by changing social group, suggesting that advancement is limited by opportunity. Perhaps males increasing in rank can only do so at sufficiently low population densities, or if new flock home ranges become available. Experimental removal studies would yield information about how social opportunities affect changes in social status between years.

A third possibility is that changes in rank are a passive process. Birds moving to vacant areas (a situation that could be facilitated during years of low population density) could attain high rank when they are joined by less experienced, yearling birds. Indeed, the majority of birds increasing in rank dominated yearlings the next year. However, this pattern would not explain how some males that advanced to high rank dominated opponents the same age or older, nor why some birds whose superiors all died remained at low rank.

The factors influencing first-year dominance status are still unknown. Flocks where the highest-ranking male was a yearling did not differ in size or composition from flocks where the highest-ranking bird was an adult (K. A. Schubert, unpubl. data). An understanding of social rank in chickadees truly requires an understanding of flock formation. Although Smith (1991) has made many observations of this process, all systematic studies of chickadee dominance behaviour have taken place after flock formation. Future studies should focus on the process of flock formation and the correlates of social dominance within newly formed flocks.

INDIVIDUAL VARIATION IN REPRODUCTIVE SUCCESS

Male and female LRS was similar, but the standardized variance based on population-level estimates was greater in males. The greater variance among males may arise because many do not breed in their first year, and because annual reproductive success increases with age (Table 1). Female chickadees have significantly shorter life expectancies than males (K. A. Schubert, unpubl. data), which would contribute to lower variance among females (Newton, 1989). Our models showed that lifespan is the best predictor of breeding success and LRS in successfully breeding individuals of both sexes, a pattern consistent with observations in other bird species (Newton, 1989).

Several studies have shown subtle effects of individual attributes such as body size on LRS (Bryant, 1989; Mills, 1989; but see also McCleery & Perrins, 1988). Previous results support the idea that dominance should also influence LRS. In song sparrows (*Melospiza melodia*), dominance in yearlings is related to territory acquisition (Arcese & Smith, 1985), which in turn predicted a male's LRS (Smith & Arcese, 1989). A similar pattern was observed in Siberian jays (*Perisoreus infaustus*), where delayed dispersal was associated with dominance among siblings (Ekman, Eggers & Griesser, 2002), and males delaying dispersal had greater LRS than dispersing yearlings (Ekman, Bylin & Tegelstrom, 1999).

We found some evidence that rapid rank acquisition enhances male fitness. Our results confirmed the relationship between male rank and annual reproductive success shown in previous studies on this population (Otter *et al.*, 1998, 1999; Mennill *et al.*, 2004). We expected to find the same pattern on a lifetime level. When considering only males that bred successfully, there was no relationship between rank and LRS. However, low-ranking males did have lower LRS when including observations of birds that failed to breed. One possibility is that the benefit of high rank is weaker than the magnitude of stochastic differences in breeding success. We could not control for year effects due to small sample sizes and missing data; this may have confounded our results. It may also be that some variation in LRS was not captured in our dataset. For example, we did not have data on whether rank influenced the probability of nest failure before day six. Similarly, our analyses did not address variation in fledging success, which is a key component of LRS. Our results point to rank-related differences in LRS, but would be strengthened by additional measures of reproductive success.

CONCLUSION

Descriptive studies of the process of social rank acquisition provide insights for the evolution of sociality. The dominance-structured social system of black-capped chickadees differs from those of many cooperative breeders because low-ranked individuals are not excluded from breeding, and there is high turnover between years. Surviving low-ranked males stand a good chance of advancing to high rank between years;

thus, they are likely hopeful dominants, tolerating subordination early in life as they wait for advantages that accompany high social status. This is the first study to investigate long-term reproductive output in black-capped chickadees, and one of the first avian studies to investigate the influence of social dominance on fitness in a noncooperative breeder. Rank in male chickadees is a dynamic trait increasing with age and linked to flock membership. High rank enhances annual reproductive success. We found some evidence that rapid rank acquisition increases male LRS; however, this by no means explains the entire pattern of fitness variation.

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