2008

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Recommended Citation

Schubert, Kristin A.; Mennill, Daniel J.; Ramsay, Scott M.; Otter, Ken A.; Ratcliffe, Laurene M.; and Kraus, Cornelia, "Between-year survival and rank transitions in male black-capped chickadees (Poecile atricapillus): A multistate modeling approach" (2008). *Auk*, 125, 3, 629-636.
https://scholar.uwindsor.ca/biologypub/1045

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Source: The Auk, 125(3):629-636.
Published By: The American Ornithologists' Union
https://doi.org/10.1525/auk.2008.07092
URL: http://www.bioone.org/doi/full/10.1525/auk.2008.07092

The Auk 125(3):629–636, 2008
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Printed in USA.

BETWEEN-YEAR SURVIVAL AND RANK TRANSITIONS IN MALE BLACK-CAPPED CHICKADEES (*POECILE ATRICAPILLUS*): A MULTISTATE MODELING APPROACH

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Abstract.—In dominance-structured animal societies, variation in individual fitness is often related to social status. Like many passerine birds, Black-capped Chickadees (*Poecile atricapillus*) have a short average adult life-expectancy (~2 years); however, the maximum recorded life span is >5× as long. Enhanced annual survival could contribute to greater lifetime reproductive success for male Black-capped Chickadees with high social rank. We used multistate capture–mark–recapture models to estimate annual survival of male Black-capped Chickadees in Ontario using resighting and recapture data collected from 1997 to 2002. Our goal was to evaluate support for an influence of rank on annual survival and estimate its effect size for a food-supplemented study site. We also statistically modeled the probability of between-year rank transitions. Model selection based on Akaike's information criterion provided support for an effect of rank on survival. However, multimodel inference revealed that the size of the effect was rather small. Over the six study years, model-averaged estimates of the survival benefit of high versus low rank ranged from 5.0 to 7.3%. As expected, survival was strongly year-dependent, with model-averaged estimates of annual survival probability varying between 0.36 and 0.73. Age was an important predictor of the probability of rank transitions. Low-ranked second-year birds were less likely than older low-ranked birds to advance to high rank between years; likewise, high-ranked after-second-year birds were less likely to drop in rank. Other studies have found larger effects of rank on survival than we observed here. Future research should consider how interactions between social and environmental factors influence annual survival. *Received 22 June 2007, accepted 19 November 2007.*

Key words: age-specific mortality, Black-capped Chickadee, capture–mark–recapture models, Paridae, *Poecile atricapillus*, rank acquisition, social dominance.

Survie interannuelle et transitions de rang chez les *Poecile atricapillus* mâles : une méthodologie de modélisation à états multiples

Résumé.—Dans les sociétés animales structurées sur la dominance, la variation du fitness individuel est souvent liée au statut social. Comme plusieurs passereaux, *Poecile atricapillus* a une courte espérance de vie adulte moyenne (~2 ans). Toutefois, la durée de vie maximale enregistrée est >5× plus longue. Une survie annuelle accrue pourrait contribuer à un succès reproducteur à vie supérieur pour les mâles de haut rang social. Nous avons utilisé des modèles de capture–marquage–recapture à états multiples afin d'estimer la survie annuelle de *P. atricapillus* mâles en Ontario en utilisant des données de ré-observation et de recapture récoltées entre 1997 et 2002. Notre objectif était d'évaluer l'influence du rang sur la survie annuelle et d'estimer la taille d'effet sur un site d'étude de nourrissage. Nous avons aussi modelé statistiquement la probabilité des transitions de rang entre les années. La sélection des modèles basée sur le critère d'information d'Akaike a supporté l'hypothèse d'un effet du rang sur la survie. Cependant, l'inférence multi-modèle a révélé que la taille d'effet était plutôt petite. Au cours des six années de l'étude, les estimations moyennes du profit de la survie d'un rang élevé versus faible variait de 5,0 à 7,3%. Tel qu'attendu, la survie était fortement dépendante de l'année, avec des estimations moyennes de la probabilité de survie annuelle variant entre 0,36 et 0,73. L'âge était un indice important de la probabilité

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The Auk, Vol. 125, Number 3, pages 629–636. ISSN 0004-8038, electronic ISSN 1938-4254. © 2008 by The American Ornithologists' Union. All rights reserved. Please direct all requests for permission to photocopy or reproduce article content through the University of California Press's Rights and Permissions website, http://www.ucpressjournals.com/reprintInfo.asp. DOI: 10.1525/auk.2008.07092

des transitions de rang. Les oiseaux de deuxième année de rang inférieur avaient moins tendance à accéder à des rangs supérieurs que les oiseaux plus âgés de rang inférieur entre les années. De même, les oiseaux de plus de deux ans et de haut rang avaient moins tendance à régresser. D'autres études ont trouvé des effets du rang sur la survie plus importants que ce que nous avons observé. Les recherches futures devraient s'attarder sur la façon dont les interactions entre les facteurs sociaux et environnementaux influencent la survie annuelle.

Variation in annual survival is a key source of differential fitness in many species (Lahti et al. 1998). Social interactions can influence many of the factors that mediate survival. Consequently, survivorship may vary not only with characteristics of the natural environment (Clobert et al. 1988) but also with competitive relationships among conspecifics (Lahti 1998). Understanding the relationship between social dominance and annual survival can help in explaining the evolution and persistence of dominance-based behavioral strategies. This is especially true for species in which variability in individual fitness has already been well studied.

Dominance-structured social groups are common in birds (Piper 1997). As in many taxa (Ellis 1995), there is a strong positive relationship between social status and reproductive success across avian species (Piper 1997), and it has also been suggested that high rank enhances individual survival. However, the relationship between social status and mortality risk may be complex. On one hand, there is substantial evidence that dominant birds survive better in winter (e.g., Lahti 1998), which is arguably the harshest season for passerine birds in the temperate zone (Pravosudov and Grubb 1997). On the other hand, annual survival does not depend on winter events alone. High-ranked individuals may experience greater mortality during the breeding season, for instance through increased predation risk (Krams 2001).

Studies of annual survival are of interest because fitness is highly dependent on longevity, not just seasonal survival (Newton 1989). We can determine whether dominant animals actually fare better from one year to the next by investigating patterns of annual survivorship in relation to social rank over several years.

We investigated annual survival in a six-year study of the Black-capped Chickadee (*Poecile atricapillus*; hereafter "chickadee"), a small (9–12 g) nonmigratory parid resident throughout northern North America. Chickadees spend the winter in flocks of 3–12 individuals that have stable membership from fall through spring of each year. Flock stability may be attributable to associations between breeding pairs (Lemmon et al. 1997), which typically consist of birds from the same winter flock (Ficken et al. 1981, Smith 1991). Chickadee flocks are characterized by linear dominance hierarchies among male flock-mates (Smith 1991), and there is ample evidence of rank-related benefits for individual males. Dominant males outcompete their flock-mates for food, foraging sites, and roosting sites in winter (Desrochers 1989). They may be less vulnerable to predation (Zanette and Ratcliffe 1994), and one study found greater overwinter survival for high-ranked males (Desrochers et al. 1988). Dominant males show improved territory acquisition (Desrochers et al. 1988) and territory size (Mennill et al. 2004). High social status enhances fitness through greater hatching and fledging success of young (Otter et al. 1999) and higher rates of genetic paternity (Otter et al. 1998, Mennill et al. 2004). Dominant males are also preferred as the new mates of females that divorce (Otter and Ratcliffe 1996, Ramsay et al. 2000).

In a previous analysis of long-term data on this chickadee population, we evaluated the influence of patterns of rank acquisition on lifetime reproductive success (LRS; Schubert et al. 2007). In the present study, we used capture–mark–recapture models to investigate correlates of annual survival and rank transitions. We first asked whether high social status leads to greater annual survival in male chickadees, estimating the survival difference between high- and low-ranked males and the statistical effect size of these differences. Because age and rank are known to be correlated among male chickadees (few individuals attain high rank in their first year of life), we used model selection under the information-theoretic paradigm to judge their relative importance for annual survival. Our second question dealt with the process of rank acquisition. Expanding our previous finding that rank tends to be stable or increase between years (Schubert et al. 2007), we employed multistate models to estimate rank-transition probabilities of each age- and rank-class of birds. In short, we asked which individuals were most likely to advance, decrease, or remain at the same rank between years.

Methods

Study area and population.—Chickadees at the Queen's University Biological Station near Chaffey's Lock, Ontario (44°34′N, 76°19′W), have been studied since 1988. Our analyses included individual records from 1997–2002, because data from earlier years were collected using a much smaller study area. The 2-km^2 field site comprised a forested peninsula bordered by a lake, as well as two small islands <200 m from shore. Habitat was mainly mature second-growth forest (*Acer* spp., *Quercus* spp., *Pinus* spp., *Betula papyrifera*) interspersed with old fields and small streams. Winter temperatures ranged from −40 to 5°C, averaging around −5°C throughout January and February; the ground was typically snow-covered from December through March.

Field methods.—From January through March each year, birds were attracted to between 11 (in 1997) and 15 (in 2002) feeding stations baited with black oil sunflower seeds. Feeders were dispersed across the entire study site, which gradually increased in area over the six study years (as in Koivula et al. 1996). Feeders were always filled, so birds had constant access to food at these sites. In January and February, we caught all birds at the feeding stations using Potter's traps. Individuals were marked with numbered aluminum Canadian Wildlife Service bands (Environment Canada banding sub-permits 10302 AK/AP/AW/BE) and one to three plastic color bands in unique combination (there is no evidence of color-band loss in chickadees). Between 57 and 95 males were captured each year (mean = 74.3 ± 6.2 [SE]), of which 59% were unbanded at the time. We used rectrix shape and wear to distinguish unbanded birds that had fledged the previous season and were entering their second year of life (SY) from older birds (after-second-year, ASY); ~20% of unbanded birds caught annually were classified as ASY. Technically, birds in both age classes were mature adults by the time of trapping. Newly banded birds were sexed with a discriminant function analysis of body mass, wing, and tail length (Desrochers 1989), and sexes were later confirmed from breeding behavior, by molecular methods, or both (~50% of males were sexed by molecular methods) (Ramsay et al. 2003). Analyses presented here deal exclusively with male chickadees, because the nature of social relationships in female chickadees is poorly understood (but see Smith 1991, Ramsay and Ratcliffe 2003).

Rank-determination and resighting data.—Around February of each year, when the catching period was over, feeding stations were replaced with dominance boards (0.5-m-diameter circles with a food hopper on one end). We scored dominance relationships between dyads based on competitive interactions for seeds. Males were identified as dominant in a single interaction when they (1) supplanted or chased an opponent, (2) successfully resisted a supplanting attack, (3) elicited a submissive posture in another individual, or (4) fed while an opponent waited to approach (Otter et al. 1998). Interactions at feeders were representative of relationships between flock-mates at other sites during winter (Smith 1991, D. J. Mennill unpubl. data). The period during which dominance data were collected was later used as the resighting occasion in our models (see below).

Dominance was scored in the context of stable winter flocks. We defined "flocks" ($n = 123$ from 1997–2002; mean = 20.5 ± 1.9 [SE] flocks year^{-1}) as groups of birds consistently observed together and associating in the absence of other birds. We compiled the outcomes of all 2,241 dyadic dominance interactions between male flock-mates (range: 1–24 interactions dyad^{-1}, mean = 3.0 ± 0.1) and constructed linear dominance hierarchies with MATMAN (de Vries 1998; Noldus Information Technology, Wageningen, The Netherlands). In such a hierarchy, each individual has a clear relationship as either dominant or subordinate to every other male member of its flock. On the basis of these hierarchies, we assigned males to nominal within-flock classes of high (H) and low (L) rank. We assigned high rank to the top male in a flock containing two or three males, the top two males in a flock of four or five males, and the top three in a flock of six males. All other males were designated as low-ranked.

There were not enough mid-ranked birds to include a third state in our models. Rather than omitting these birds from analysis, we included them in the same category as low-ranked males; this allowed us to calculate rank transitions between years without losing observations. We grouped mid-ranked males with low-ranked ones because of previous evidence that their behavior might be similar; Zanette and Ratclifffe (1994) found that mid-ranked birds behave like low-ranked individuals in risk-taking near simulated predators. Also, both mid- and low-ranked males receive aggressive attacks from high-ranked males, whereas high-ranked males usually initiate attacks (D. J. Mennill unpubl. data). Grouping mid- and low-ranked males may have made our estimates of rank-related survival differences more conservative. Rank-advancement probabilities would be somewhat underestimated if SY birds were more likely to become mid-ranking than high-ranking.

We operationally defined a "resighting event" as a year in which both the age category and the social rank of an individual were known. For the purpose of our models, a bird could be resighted (or not) once annually, at a rank of low or high and an age of SY or ASY. The resighting period was restricted to the time of year when dominance observations were made, with a median date, averaged over all years, of 4 March (range: 45–69 days, mean = 63.2 ± 3.7 [SE] days). Analyses included 323 (re)sightings of 184 individual male birds. Our models could not distinguish whether disappearances indicated mortality or emigration. Chickadees are highly philopatric during adulthood (Brittingham and Temple 1988, Smith 1991). However, estimates of age-related mortality would have been biased if SY males emigrated to find breeding territories and failed to return the following winter.

Modeling outline.—To estimate annual survival and rank-transition probabilities, we employed multistate capture–mark–recapture models (also known as multistratum models; Arnason 1972, 1973; Hestbeck et al. 1991; Brownie et al. 1993; Schwarz et al. 1993). The states in these models can be discrete locations or individual attributes such as social rank. An important assumption of these models is that the animal's probability of state transition between time i and $i + 1$ depends only on its state at time i (i.e., can be described as a first-order Markov process). We chose the parameterization implemented in MARK (White and Burnham 1999), which, to separate survival (S) and movement (Ψ) between different states, additionally assumes that survival from time i to $i + 1$ does not depend on the state at time $i + 1$. Thus, technically, the animal survives first, and, immediately before time $i + 1$, either changes state or stays in its previous state (Nichols et al. 1994).

Resighting events have a specific operational definition in the present study (see above). A bird was recorded as resighted in a given year if we could determine its social rank through behavioral observations and its age category was known. A few males were seen at least once during the winter but could not be ranked. Usually, this occurred if we observed a male at a feeder but did not know its flock membership. Including these birds in the analysis as "not seen" for the given encounter occasion would underestimate actual resighting probabilities. To prevent this, we treated them as "losses on capture" for the last time they were ranked and as "new captures" the next time they were observed and ranked; there were 18 such cases in our data set. The initial collection of rank data was unbiased, given that ranked birds were always observed in the context of winter flocks with stable membership.

Model selection was based on Akaike's information criterion (AIC) and followed the analysis strategies outlined by Burnham and Anderson (2002). This entailed constructing only biologically plausible models *a priori*, rather than modeling all possible combinations of variables. All of our candidate models were nested within the global model. We used the median-$\hat{c}$ procedure provided by MARK to assess the goodness-of-fit (GOF) of our global model to the data and to estimate the overdispersion parameter c. Given that the global model fits the data, all candidate models with a lower AIC also provide an adequate fit (i.e., are more parsimonious). Additional GOF-testing with the program U-CARE (Choquet et al. 2003, Pradel et al. 2003) did not identify any violation of the testable assumptions of multistate models (for all subtests provided: $P > 0.71$).

Because of the rather sparse data, we employed AIC$_c$, the small-sample variant of AIC (Anderson et al. 1994). We interpreted model-selection results in a weight-of-evidence context based on AIC$_c$ differences (Δ_i) and Akaike weights (w_i), as described by Burnham and Anderson (2002). Briefly, Δ_i is the difference between the AIC$_c$ of the top model and that of the model considered. According to Burnham and Anderson (2002), models with $\Delta_i \leq 2$ have substantial support and models with $4 < \Delta_i < 7$ achieve some support, whereas models with $\Delta_i > 10$ have little support or fail to account for some important explainable variation in the data. Given the data and the candidate set of models, Akaike weights are proportional to the relative likelihood of the model considered and are, thus, a measure of the weight of evidence that a given model is the best one in the set. They are normalized such that the AIC weights of all models in the set sum to 1 (i.e., they change if the model set is changed).

The Akaike weight of our top model (where $\Delta_i = 0$) was 0.14, well below 0.9; this suggested considerable model-selection uncertainty (i.e., the data did not allow selection of only one model, but rather several models received substantial support). Therefore, we used multimodel inference techniques as suggested by Buckland et al. (1997) and Burnham and Anderson (2002). To determine a 95% confidence subset of models, we included all models, starting from the top model, until their cumulative Akaike weights reached 0.95. The relative importance of predictor variables or structural terms was assessed by summing Akaike weights for all models of the candidate set in which the predictor was present and is given as w_+(predictor). Finally, to obtain model-averaged parameter estimates and standard errors unconditional on a given model (but still conditional on the candidate model set), the effect of a given model on the estimated parameter value was weighted according to its AIC weight, and a variance component to account for model-selection uncertainty was included (Buckland et al. 1997). Model notation follows Lebreton et al. (1992). All estimates of survival and rank-transition probabilities are reported on an annual time scale (a^{-1}).

Candidate set of models.—The list of candidate models and their biological meaning is provided in Table 1. Survival is highly variable between years for small nonmigratory passerines (Perrins et al. 1991). Therefore, all our models of survival probabilities (S) of male chickadees include an effect of year (t). In addition to rank, we considered age as a factor potentially affecting survival probabilities, because age-effects may influence survival throughout the first winter of life. We included models allowing for an additive effect of either rank (r) or age (a), as well as one allowing for additive effects of both rank and age. Finally, because it seemed plausible that age and rank could interact to influence survival probabilities, we considered one model where survival differed for all four rank–age combinations (low–SY, low–ASY, high–SY, and high–ASY) as the global model for survival.

We included only two candidate models for resighting probabilities (p). To determine the rank of a male in a given year, it was necessary to observe dyads of dominant and subordinate birds of known age. Thus, it seemed unlikely that rank or age would affect resighting probabilities. We used a model with only time-dependence (t) as our most general model for p. Additionally, because the observation period was extended until no more marked but previously unobserved birds were recorded and birds of unknown rank were treated as losses on capture (see above), we expected resighting probabilities to be high and constant. Models incorporating constant resighting probabilities were denoted as "$p.$" (p-dot).

All candidate models for rank-transition probabilities (Ψ) included an effect of current rank, because, *a priori*, the probability of rising in rank should be different from that of losing social status (Smith 1991). Following similar logic, we did not include additive models such as $r + a$ or $r + t$: such models would make the biologically implausible assumption that the probabilities of rising and falling in rank would show a parallel course on a logit scale (e.g., model $a + r$ would signify that the age class with the higher probability of rising in rank also had a higher probability of falling in rank compared with the other age class). We included age as a potential factor modulating the probability of rank acquisition and time as a proxy variable for effects of the changing population composition. We considered all combinations of parameters given in Table 1 and fit a total of 40 models. The global model in our candidate set was $S_{(r\times a)+t}\,p_t\,\Psi_{r\times(a+t)}$. A more complex model including all interaction effects would have been overparameterized given the available data.

TABLE 1. Set of candidate models: model notation and biological significance. Factors considered are rank (r), age (a), and time (t). Possible effects can be main and interactions (×) or additive only (+); global models are highlighted in bold. We tested all 40 possible models combining the parameters given below. The full model was $S_{(r\times a)+t}\,p_t\,\Psi_{r\times(a+t)}$.

Model notation	Biological significance
Survival probability S is…	
t	year-dependent
$r + t$	with an additive effect of rank
$a + t$	with an additive effect of age
$r + a + t$	with additive effects of rank and age
$(r \times a) + t$	**with an additive effect of rank interacting with age**
Resighting probability p is…	
.	constant
t	**year-dependent**
Rank-transition probability Ψ is…	
r	rank-specific
$r \times t$	with an interaction with year
$r \times a$	with an interaction with age
$r \times (a + t)$	**with an interaction with year and an additive age-effect**

RESULTS

The best-supported model in our candidate set ($S_{r+t}\,p_{.}\,\Psi_{r\times a}$; Table 2) included additive effects of rank and time on annual survival and an interactive effect of rank and age on transition probabilities between rank states. Our estimate of the variance inflation factor suggested a good fit of the global model ($\hat{c} = 0.973 \pm 0.012$ [SE]). This implies that the *a priori* selection of model terms was biologically realistic and that our data set did not violate any key assumptions. The unusually low estimate of the overdispersion factor c is probably attributable to the high resighting probability throughout the study ($\hat{p} = 1.0 \pm 0.53^{-0.5}$[SE]). In other words, very few chickadees that were still living disappeared for an entire season (in which they were neither seen nor ranked) and then reappeared. None of the models included in the 95% confidence subset of models (Table 2) supported a temporally variable resighting probability (p: $w+(t) = 0.037$). Therefore, we averaged estimates and standard errors only over models with a constant resighting probability. We took this approach because the benefit of obtaining a survival estimate for the last interval (2001 to 2002) outweighed the advantage of averaging over all models in the candidate set. This estimate

TABLE 2. Summary of model-selection statistics for the analysis of annual survival and rank-transition probabilities of male Black-capped Chickadees from 1997 to 2001. The models shown comprise a 95% confidence subset for the actual best Kullback-Leibler model based on cumulative Akaike weights and the global model (GM) at bottom (models are grouped by survival model, ordered as in Table 1). Factors considered are age (*a*), rank (*r*), and time/year (*t*). The rank of the model, the number of estimable parameters (*K*), the deviance (DEV), Akaike's information criterion for small samples (AIC_c), the difference between the minimum AIC_c of the top model and the model considered (Δ_i) and Akaike weights (w_i) are given for each model. The best approximating model of the candidate set (based on AIC_c) is highlighted in bold. See Table 1 for abbreviations.

Rank	Model	*K*	DEV	AIC_c	Δ_i	w_i
10	$S_t p_. \Psi_r$	8	142.00	507.00	2.50	0.04
7	$S_t p_. \Psi_{r \times t}$	16	123.74	506.41	1.91	0.05
3	$S_t p_. \Psi_{r \times a}$	10	136.20	505.50	1.01	0.08
5	$S_t p_. \Psi_{r \times (a+t)}$	18	118.59	505.85	1.36	0.07
6	$S_{r+t} p_. \Psi_r$	9	138.81	505.95	1.46	0.07
4	$S_{r+t} p_. \Psi_{r \times t}$	17	120.55	505.51	1.01	0.08
1	$\boldsymbol{S_{r+t} p_. \Psi_{r \times a}}$	**11**	**133.01**	**504.50**	**0.00**	**0.14**
2	$S_{r+t} p_. \Psi_{r \times (a+t)}$	19	115.40	504.99	0.49	0.11
17	$S_{a+t} p_. \Psi_r$	9	141.02	508.17	3.67	0.02
13	$S_{a+t} p_. \Psi_{r \times t}$	17	122.77	507.72	3.23	0.03
9	$S_{a+t} p_. \Psi_{r \times a}$	11	135.22	506.71	2.22	0.05
11	$S_{a+t} p_. \Psi_{r \times (a+t)}$	19	117.61	507.21	2.71	0.04
16	$S_{r+a+t} p_. \Psi_r$	10	138.81	508.12	3.62	0.02
14	$S_{r+a+t} p_. \Psi_{r \times t}$	18	120.55	507.82	3.32	0.03
8	$S_{r+a+t} p_. \Psi_{r \times a}$	12	133.01	506.69	2.20	0.05
12	$S_{r+a+t} p_. \Psi_{r \times (a+t)}$	20	115.40	507.34	2.84	0.03
19	$S_{(r \times a)+t} p_. \Psi_{r \times t}$	19	119.49	509.08	4.58	0.01
15	$S_{(r \times a)+t} p_. \Psi_{r \times a}$	13	131.94	507.84	3.35	0.03
18	$S_{(r \times a)+t} p_. \Psi_{r \times (a+t)}$	21	114.33	508.64	4.14	0.02
37 (GM)	$S_{(r \times a)+t} p_t \Psi_{r \times (a+t)}$	24	114.33	515.86	11.36	0.0005

would not have been possible with parameter-redundant, fully time-dependent models.

Annual survival.—The best-supported model included an effect of rank on annual survival probabilities of male chickadees. However, only four of the seven models with $\Delta_i < 2$ provided support for a rank-effect, which suggests that rank had only a small influence on survival. Rank was almost twice as important as age in predicting annual survival probability ($w + (r) = 0.61$, $w + (a) = 0.34$; $0.61/0.34 = 1.79$); none of the well-supported models ($\Delta_i \le 2$) contained an age-effect on survival.

Model-averaged estimates showed a pattern of fluctuating annual survival, with high-ranked males surviving somewhat better than low-ranked males (Fig. 1). Overall, annual survival fluctuated between 36 and 73% and was lowest between 1998 and 1999. The geometric mean survival probability of high-ranked males was 0.552, as compared with 0.487 for low-ranked males. There was no notable difference in geometric mean survival between SY (0.526) and ASY (0.537) birds across years. In summary, annual survival was mainly influenced by time (year). Rank was responsible for a 6.5% survival difference, whereas age played a negligible role in this data set.

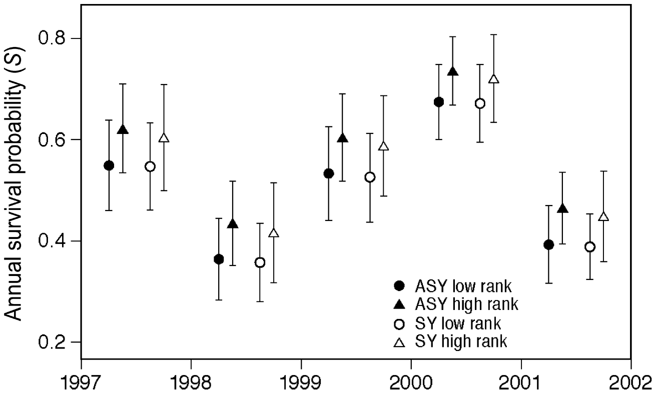

FIG. 1. Annual survival probabilities for male Black-capped Chickadees from 1997 to 2002. Model-averaged estimates and their unconditional standard errors are depicted. Group means for each period have been spaced for clarity.

Rank transitions.—Model-selection results supported an age-effect on rank-transition probabilities (Table 2). The top model contained an interaction between current rank and age ($\Psi_{r \times a}$): ASY males were more likely to rise in rank, and less likely to drop in rank, than SY males. The almost equally well supported second-best model ($\Delta_i = 0.49$) suggested an additive effect of year. Age was relatively more important as a predictor of rank transitions than time ($w + (a) = 0.62$, $w + (t) = 0.48$). However, again, only four of the seven best-supported models contained an effect of age on rank transitions.

Probably as a consequence of high yearly turnover of males, the chance of rising in rank was rather high (Fig. 2), ranging from 55 to 74% for ASY males (geometric mean 60.1%) and from 42 to 63% for SY males (geometric mean 47.3%). High-ranked males were usually able to maintain their social status. High-ranked ASY males had a geometric mean risk of dropping in rank of only 10.2%, whereas for dominant SY males, the risk was almost twice as high (27.3%).

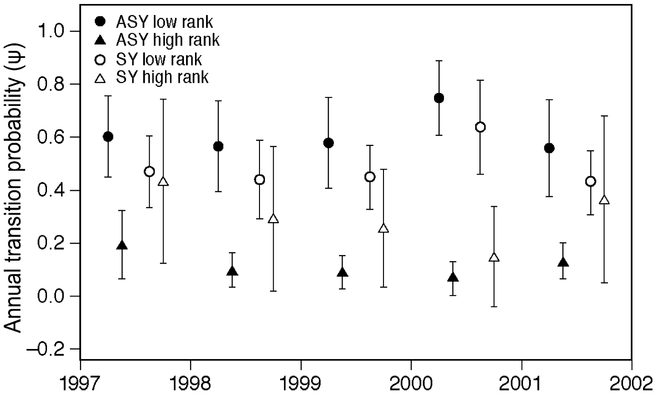

FIG. 2. Rank-transition probabilities for male Black-capped Chickadees from 1997 to 2002. Model-averaged estimates and their unconditional standard errors are depicted. Group means for each period have been spaced for clarity.

Discussion

As expected, rates of annual survival varied greatly across the six years of our study. We found some support for an additive, positive effect of high rank on survival. The magnitude of between-year differences demonstrates that environmental variability plays a substantial role in mediating individual survival. Rank-effects on survival were not large in this data set (only 6.5%). Still, survival was better explained by models incorporating a rank-effect. This suggests that high-ranked males survive somewhat better as a result of their status. After-second-year males were more likely than SY birds to increase in rank between years and less likely to lose their high status, which is consistent with the idea that rank-advancement depends on site seniority or competitive experience.

Annual survival.—Overall, annual survival rates of males in our chickadee population agree with other published results, particularly those of Loery et al. (1997), who reported an average survival probability of 0.62 over 35 years for their Connecticut chickadee study population. A 15-year study of Tufted Titmice (*Parus bicolor*) similarly placed annual survival rates around 0.62 (Elder 1985). Estimates of chickadee overwinter survival on food-supplemented (0.69) and unsupplemented (0.37) sites also agree with our estimates (Brittingham and Temple 1988). In parids, it is common for survival probabilities to vary more than twofold between years. Documented values for chickadees range from 0.37 to 0.90 (Loery et al. 1997). In this context, our observations of annual survival rates between 0.36 and 0.73 fall well within expected ranges.

Because the observations we used were made from January through March, we did not expect to find a strong effect of age on annual survival. Parid yearling mortality should be highest immediately after fledging (Smith 1967) and in the first winter of life (Ekman 1984). We modeled survival of birds that had already reached their first winter; thus, we missed the critical period of juvenile mortality. Furthermore, any remaining differences in winter survival of SY vs. ASY males may be related to social status. Some earlier studies that found age-effects on winter survival implicitly attributed them to differences in rank (Ekman et al. 1981, Ekman and Askenmo 1984, Hogstad 1988). Given that age and rank are closely related, it may simply be that rank is more important for survival than age.

At 6.5%, the rank-effect we observed on annual survival was rather small. Could it contribute, nonetheless, to enhanced fitness for socially dominant birds? In our earlier long-term study on the relationship between individual rank history and fitness, we showed that longevity is the best predictor of LRS in chickadees (Schubert et al. 2007). A modest increase in annual survival would be beneficial to high-ranked males. Furthermore, rank may have played a stronger role than we could detect here. Although rank changes occur in fall, at the onset of cold weather (Smith 1991), we analyzed survival on a winter–winter time scale because trapping required snow cover. The timing of data collection may have led to conservative estimates of rank-effects.

Nonetheless, other studies on passerines have shown larger survival benefits for high rank, both on an annual scale (De Laet 1985, Koivula et al. 1996) and during the winter months (Desrochers et al. 1988, Lahti et al. 1997, Lahti 1998). Dominant Song Sparrows (*Melospiza melodia*) survive 22–35% better annually than subordinates (Arcese and Smith 1985). Piper and Wiley (1990) also showed that dominance significantly predicted return rate in White-throated Sparrows (*Zonotrichia albicollis*). Factors other than rank may be more important determinants of annual survival in male chickadees.

An alternative explanation for our results is that the presence of feeders may have buffered rank-related differences in survival. Studies in several parid species have shown enhanced overwinter survival on food-supplemented sites (Jansson et al. 1981, Källander 1981, Brittingham and Temple 1988, Doherty and Grubb 2002). Food resources may be particularly important during a limited number of harsh winter days, so perhaps having access to feeders at these critical times improved survival of subordinate birds. Without comparisons with feeder-free sites, we cannot determine whether this was the case. Therefore, studies of the effects of food availability on the survival benefit of high social rank are needed. It would be interesting to conduct future studies on both supplemented and unsupplemented sites, or to reduce the regularity with which food was available. Comparisons of this kind could be expanded to investigate the relative importance of food supplementation in poor or harsh years compared with years in which natural food was abundant.

Transitions between ranks.—Researchers have long been interested in the mechanisms that underlie changes in and maintenance of social status (Schjelderup-Ebbe 1922). We have previously shown that social rank is highly correlated between years but also tends to increase over time (Schubert et al. 2007); present estimates of rank-transition probabilities confirm this finding. Most evidence suggests that subordinate chickadees are "hopeful dominants" (West-Eberhard 1975, Wiley et al. 1999). We favor the idea that rank-maintenance results from stable relationships between familiar birds (Wiley et al. 1999). Males increase in rank under changing social circumstances, and they tend to dominate new recruits (SYs).

We found that ASY low-ranked males were somewhat more likely to rise to high rank than SY low-ranked males. Likewise, rates of rank decrease were higher for SY than for ASY chickadees. This age-effect is probably related to the mode of rank advancement, which can take two typical forms in male chickadees (Schubert et al. 2007). Males may rise in rank if a formerly dominant bird ("superior") dies, or they may, alternatively, rise in rank when flock memberships change between years. The first scenario may depend on site seniority (Cristol et al. 1990, Piper 1997), which could partly explain why birds stay in one area rather than moving a few kilometers away. Individual experience could also be important for birds rising in rank when flock memberships change (Piper and Wiley 1989). Arcese and Smith (1985) showed that Song Sparrows released from captivity obtained a rank appropriate to their age rather than their tenure on site. Most male chickadees advancing in rank dominate incoming—and unfamiliar—yearlings (Schubert et al. 2007); experience likely gives older low-ranked males a better chance of dominance in new flocks.

Both site seniority and experience may explain why ASY male chickadees are more likely to increase in rank than SY birds. In both routes to rank advancement, population density and composition should also affect rank advancement. A year of high adult mortality followed by good fledgling recruitment might not show age-effects on rank transitions, given that all surviving birds will have the opportunity to advance in rank. However, in poor recruitment years, only ASY males inheriting flock territories may rise in status. Younger low-ranked males changing flocks may not be able to advance if there are no recruits to join them as subordinates. This could be the reason we found such high rates of rank advancement for both

SY and ASY low-ranked birds from 2000 to 2001, which featured a large cohort of new recruits from the 2000 breeding season.

Social rank is an important component of variation in individual fitness of male chickadees. The present results suggest that our understanding of the factors affecting annual mortality would be improved by studying the relationship between individual attributes and environmental variables. The effects of rank may be modulated by factors that vary spatially and temporally. Therefore, investigating interactions between rank and parameters such as population density, weather, food availability, and predation pressure is a promising direction for future study.

ACKNOWLEDGMENTS

We thank D. Aiama, A. Boon, P. Christie, B. Chruszcz, C. Cliffe, E. Coleman, L. Colgan, S. Cosh, M. Cunningham, R. DeBruyn, S. Doucet, J. Fotheringham, M. French, J. Hodson, C. James, A. MacDougall, P. Martin, C. McDonald, W. McLeish, B. Meigs, V. Muehter, A. Nirwal, S. Rice, T. Talvila, J. Vachon, N. Vreeswyck, and L. Webster for assistance in data-collection. The Curtis, Monaghan, Toohey, Warren, Weatherhead-Metz, and Zink families provided access to property. Queen's University Biological Station provided logistical support. Funding for the study was provided by research grants and a collaborative grant from the Natural Sciences and Engineering Research Council (NSERC), by student grants from the American Museum of Natural History, American Ornithologists' Union, Animal Behaviour Society, Association of Field Ornithologists, John K. Cooper Foundation, Sigma Xi, and Society of Canadian Ornithologists; by donations from E. and I. Ramsay and PPG Canada Inc.; and by scholarships from Queen's University, the Ontario Graduate Scholarships (OGS) Program, and NSERC. C.K. was funded by the University of Bielefeld and the Deutsche Forschungsgemeinschaft. K.A.S. received additional support from the Deutscher Akademischer Austauschdienst, as well as travel support from the University of Groningen's BCN Research School. We thank S. Doucet, K. Swiston, and S. Topp for comments on the manuscript and N. Dingemanse for critical discussion. Many additional reviewer comments improved the quality of this manuscript.

LITERATURE CITED

ANDERSON, D. R., K. P. BURNHAM, AND G. C. WHITE. 1994. AIC model selection in overdispersed capture–recapture data. Ecology 75:1780–1793.

ARCESE, P., AND J. N. M. SMITH. 1985. Phenotypic correlates and ecological consequences of dominance in Song Sparrows. Journal of Animal Ecology 54:817–830.

ARNASON, A. N. 1972. Parameter estimates from mark–recapture experiments on two populations subject to migration and death. Researches on Population Ecology 13:97–113.

ARNASON, A. N. 1973. The estimation of population size, migration rates and survival in a stratified population. Researches on Population Ecology 15:1–8.

BRITTINGHAM, M. C., AND S. A. TEMPLE. 1988. Impacts of supplemental feeding on survival rates of Black-capped Chickadees. Ecology 69:581–589.

BROWNIE, C., J. E. HINES, J. D. NICHOLS, K. H. POLLOCK, AND J. B. HESTBECK. 1993. Capture–recapture studies for multiple strata including non-Markovian transitions. Biometrics 49:1173–1187.

BUCKLAND, S. T., K. P. BURNHAM, AND N. H. AUGUSTIN. 1997. Model selection: An integral part of inference. Biometrics 53: 603–618.

BURNHAM, K. P., AND D. J. ANDERSON. 2002. Model Selection and Multimodel Inference: A Practical Information-theoretic Approach, 2nd ed. Springer-Verlag, New York.

CHOQUET, R., A. M. REBOULET, J. D. LEBRETON, O. GIMENEZ, AND R. PRADEL. 2005. U-Care 2.2 User's Manual. [Online.] CEFE/CNRS, Montpellier, France. Available at www.cefe.cnrs.fr/biom/logiciels.htm.

CLOBERT, J., C. M. PERRINS, R. H. MCCLEERY, AND A. G. GOSLER. 1988. Survival rate in the Great Tit *Parus major* in relation to sex, age, and immigration status. Journal of Animal Ecology 57:287–306.

CRISTOL, D. A., V. NOLAN, JR., AND E. D. KETTERSON. 1990. Effect of prior residence on dominance status of Dark-eyed Juncos, *Junco hyemalis*. Animal Behaviour 40:580–586.

DE LAET, J. V. 1985. Dominance and aggression in juvenile Great Tits, *Parus major* L. in relation to dispersal. Pages 375–380 *in* Behavioural Ecology: Ecological Consequences of Adaptive Behaviour (R. M. Sibley and R. H. Smith, Ed.). Blackwell Scientific, Oxford, United Kingdom.

DE VRIES, H. 1998. Finding a dominance order most consistent with a linear hierarchy: A new procedure and review. Animal Behaviour 55:827–843.

DESROCHERS, A. 1989. Sex, dominance, and microhabitat use in wintering Black-capped Chickadees: A field experiment. Ecology 70:636–645.

DESROCHERS, A., S. J. HANNON, AND K. E. NORDIN. 1988. Winter survival and territory acquisition in a northern population of Black-capped Chickadees. Auk 105:727–736.

DHONDT, A. A. 1989. Blue Tit. Pages 15–33 *in* Lifetime Reproduction in Birds (I. Newton, Ed.). Academic Press, London.

DOHERTY, P. F., JR., AND T. C. GRUBB, JR. 2002. Survivorship of permanent-resident birds in a fragmented forested landscape. Ecology 83:844–857.

EKMAN, J. 1984. Density-dependent seasonal mortality and population fluctuations of the temperate-zone Willow Tit (*Parus montanus*). Journal of Animal Ecology 53:119–134.

EKMAN, J. B., AND C. E. H. ASKENMO. 1984. Social rank and habitat use in Willow Tit groups. Animal Behaviour 32:508–514.

EKMAN, J., G. CEDERHOLM, AND C. ASKENMO. 1981. Spacing and survival in winter groups of Willow Tit *Parus montanus* and Crested Tit *P. cristatus*—A removal study. Journal of Animal Ecology 50:1–9.

ELDER, W. H. 1985. Survivorship in the Tufted Titmouse. Wilson Bulletin 97:517–524.

ELLIS, L. 1995. Dominance and reproductive success among non-human animals: A cross-species comparison. Ethology and Sociobiology 16:257–333.

FICKEN, M. S., S. R. WITKIN, AND C. M. WEISE. 1981. Associations among members of a Black-capped Chickadee flock. Behavioral Ecology and Sociobiology 8:245–249.

FORSTMEIER, W., B. KEMPENAERS, A. MEYER, AND B. LEISLER. 2002. A novel song parameter correlates with extra-pair paternity and reflects male longevity. Proceedings of the Royal Society of London, Series B 269:1479–1485.

HESTBECK, J. B., J. D. NICHOLS, AND R. A. MALECKI. 1991. Estimates of movement and site fidelity using mark–resight data of wintering Canada Geese. Ecology 72:523–533.

Hogstad, O. 1988. The influence of energy stress on social organization and behaviour of Willow Tits *Parus montanus*. Fauna Norvegica, Series C 11:89–94.

Jansson, C., J. Ekman, and A. von Brömssen. 1981. Winter mortality and food supply in tits *Parus* spp. Oikos 37:313–322.

Källander, H. 1981. The effects of provision of food in winter on a population of the Great Tit *Parus major* and Blue Tit *P. caeruleus*. Ornis Scandinavica 12:244–248.

Koivula, K., M. Orell, and S. Rytkönen. 1996. Winter survival and breeding success of dominant and subordinate Willow Tits *Parus montanus*. Ibis 138:624-629.

Krams, I. 2001. Perch selection by singing chaffinches: A better view of surroundings and the risk of predation. Behavioral Ecology 12:295–300.

Lahti, K. 1998. Social dominance and survival in flocking passerine birds: A review with an emphasis on the Willow Tit *Parus montanus*. Ornis Fennica 75:1–17.

Lahti, K., K. Koivula, and M. Orell. 1997. Dominance, daily activity and winter survival in Willow Tits: Detrimental cost of long working hours? Behaviour 134:921–939.

Lahti, K., M. Orell, S. Rytkönen, and K. Koivula. 1998. Time and food dependence in Willow Tit winter survival. Ecology 79:2904–2916.

Lebreton, J.-D., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: A unified approach with case studies. Ecological Monographs 62:67–118.

Lemmon, D., M. L. Withiam, and C. P. L. Barkan. 1997. Mate protection and winter pair-bonds in Black-capped Chickadees. Condor 99:424–433.

Loery, G., J. D. Nichols, and J. E. Hines. 1997. Capture–recapture analysis of a wintering Black-capped Chickadee population in Connecticut, 1958–1993. Auk 114:431–442.

Mennill, D. J., S. M. Ramsay, P. T. Boag, and L. M. Ratcliffe. 2004. Patterns of extrapair mating in relation to male dominance status and female nest placement in Black-capped Chickadees. Behavioral Ecology 15:757–765.

Newton, I., Ed. 1989. Lifetime Reproduction in Birds. Academic Press, London.

Nichols, J. D., J. E. Hines, K. H. Pollock, R. L. Hinz, and W. A. Link. 1994. Estimating breeding proportions and testing hypotheses about costs of reproduction with capture–recapture data. Ecology 75:2052–2065.

Otter, K., S. M. Ramsay, and L. Ratcliffe. 1999. Enhanced reproductive success of female Black-capped Chickadees mated to high-ranking males. Auk 116:345–354.

Otter, K., and L. Ratcliffe. 1996. Female initiated divorce in a monogamous songbird: Abandoning mates for males of higher quality. Proceedings of the Royal Society of London, Series B 263:351–355.

Otter, K., L. Ratcliffe, D. Michaud, and P. T. Boag. 1998. Do female Black-capped Chickadees prefer high-ranking males as extra-pair partners? Behavioral Ecology and Sociobiology 43:25–36.

Perrins, C. M., J.-D. Lebreton, and G. J. M. Hirons, Eds. 1991. Bird Population Studies: Relevance to Conservation and Management. Oxford University Press, Oxford, United Kingdom.

Piper, W. H. 1997. Social dominance in birds: Early findings and new horizons. Pages 125–187 *in* Current Ornithology, vol. 14 (V. Nolan, Jr., E. D. Ketterson, and C. F. Thompson, Eds.). Plenum Press, New York.

Piper, W. H., and R. H. Wiley. 1989. Correlates of dominance in wintering White-throated Sparrows: Age, sex and location. Animal Behaviour 37:298–310.

Piper, W. H., and R. H. Wiley. 1990. The relationship between social dominance, subcutaneous fat, and annual survival in wintering White-throated Sparrows (*Zonotrichia albicollis*). Behavioral Ecology and Sociobiology 26:201–208.

Pradel, R., C. M. A. Wintrebert, and O. Gimenez. 2003. A proposal for a goodness-of-fit test to the Arnason-Schwarz multisite capture–recapture model. Biometrics 59:43–53.

Pravosudov, V. V., and T. C. Grubb, Jr. 1997. Energy management in passerine birds during the nonbreeding season: A review. Pages 189–234 *in* Current Ornithology, vol. 14 (V. Nolan, Jr., E. D. Ketterson, and C. F. Thompson, Eds.). Plenum Press, New York.

Ramsay, S. M., D. J. Mennill, K. A. Otter, L. M. Ratcliffe, and P. T. Boag. 2003. Sex allocation in Black-capped Chickadees *Poecile atricapilla*. Journal of Avian Biology 34:134–139.

Ramsay, S. M., K. A. Otter, D. J. Mennill, L. M. Ratcliffe, and P. T. Boag. 2000. Divorce and extrapair mating in female Black-capped Chickadees (*Parus atricapillus*): Separate strategies with a common target. Behavioral Ecology and Sociobiology 49:18–23.

Ramsay, S. M., and L. M. Ratcliffe. 2003. Determinants of social rank in female Black-capped Chickadees (*Poecile atricapilla*). Canadian Journal of Zoology 81:117–121.

Schjelderup-Ebbe, T. 1922. Beiträge zur Sozialpsychologie des Haushuhns. Zeitschrift für Psychologie 88:225–252.

Schubert, K. A., D. J. Mennill, S. M. Ramsay, K. A. Otter, P. T. Boag, and L. M. Ratcliffe. 2007. Variation in social rank acquisition influences lifetime reproductive success in Black-capped Chickadees. Biological Journal of the Linnean Society 90:85–95.

Schwarz, C. J., J. F. Schweigert, and A. N. Arnason. 1993. Estimating migration rates using tag-recovery data. Biometrics 49:177–193.

Smith, S. M. 1967. Seasonal changes in the survival of the Black-capped Chickadee. Condor 69:344–359.

Smith, S. M. 1991. The Black-capped Chickadee: Behavioral Ecology and Natural History. Cornell University Press, Ithaca, New York.

West Eberhard, M. J. 1975. The evolution of social behavior by kin selection. Quarterly Review of Biology 50:1–33.

White, G. C., and K. P. Burnham. 1999. Program MARK: Survival estimation from populations of marked animals. Bird Study 46 (Supplement):S120–S139.

Wiley, R. H., L. Steadman, L. Chadwick, and L. Wollerman. 1999. Social inertia in White-throated Sparrows results from recognition of opponents. Animal Behaviour 57:453–463.

Zanette, L., and L. M. Ratcliffe. 1994. Social rank influences conspicuous behaviour of Black-capped Chickadees, *Parus atricapillus*. Animal Behaviour 48:119–127.

Associate Editor: C. M. Handel