

CAN SELECTION BY AN ECTOPARASITE DRIVE A POPULATION OF RED CROSSBILLS FROM ITS ADAPTIVE PEAK?

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Abstract.—The bill structures of different call types of red crossbills (*Loxia curvirostra* complex) in western North America usually approximate the predicted optima for foraging on single species of conifers. One clear exception is the call type in the South Hills, Idaho, that is coevolving in an evolutionary arms race with Rocky Mountain lodgepole pine (*Pinus contorta* ssp. *latifolia*). Although South Hills crossbills forage only on the cones of these lodgepole pines, their average bill depth is smaller than that predicted to be optimal. Because preliminary data showed that large-billed males were more likely to exhibit symptoms of ectoparasitic mite (*Knemidokoptes jamaicensis*) infestation, the goal of our study was to further quantify the incidence of mite infestation and determine whether selection by mites may have favored smaller-billed crossbills and thus driven crossbills away from the foraging optimum. We estimated annual survival of both infected and uninfected South Hills crossbills using program MARK, which allows for auxiliary variables such as bill size and sex to be included in survival analyses. Mite infestation depressed crossbill survival and, especially for males, caused directional selection against larger-billed individuals. Such selection may explain why South Hills crossbills have smaller bills than the optimum and why average bill size for males has decreased from 1998 to 2003. This selection may also explain why the degree of sexual size dimorphism has decreased by nearly 50% since 1998.

Key words.—Capture-recapture models, immunocompetence, *Knemidokoptes jamaicensis*, *Loxia curvirostra*, morphological evolution, sexual dimorphism, survivorship.

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Selection on quantitative traits is a primary cause of phenotypic evolution in wild populations (Kingsolver et al. 2001; Rieseberg et al. 2002). Consequently, a central focus of evolutionary biology is to understand the occurrence and form of selection in the wild (Endler 1986; Brodie et al. 1995). While numerous studies on natural selection exist, relatively few actually demonstrate the causes and consequences of selection. Endler (1986) attributes this dearth to a lack of long-term ecological studies of systems in which selection is being measured.

In earlier studies of red crossbills (*Loxia curvirostra* complex) coevolving with Rocky Mountain lodgepole pine (*Pinus contorta* ssp. *latifolia*), crossbills were found to exert selection on lodgepole pine (Benkman et al. 2003) and lodgepole pine was shown to evolve in response to such selection (Benkman 1999; Benkman et al. 2001, 2003). Crossbills experienced reciprocal selection for efficient foraging on lodgepole pine cones with increased defenses (Benkman 2003; Benkman et al. 2003) and, in turn, have evolved larger, deeper bills (Benkman 1999; Benkman et al. 2001, 2003). Bill depth is the trophic character most strongly correlated with foraging efficiency in crossbills (Benkman 1993; Benkman and Miller 1996) and is the trait that is a target of selection (Benkman 2003). One of the coevolving crossbill populations, the Cypress Hills crossbill, had a mean bill depth (10.01 mm) that was very similar to the predicted optimum bill depth (9.99 mm; Benkman et al. 2001); optimal bill depth is the same for both sexes and is estimated as that which minimizes the time necessary to meet daily energy demands (see Benkman

1993; Benkman and Miller 1996). The match between observed and predicted indicates that the crossbills were at a coevolutionary equilibrium with lodgepole pine; because males are larger than females, males tend to be larger than the optimum and females tend to be smaller than the optimum. As of 2003, however, another population of crossbills, the South Hills crossbill, had an average bill depth 0.15 mm less than the predicted optimal bill depth. While this latter difference might seem slight, it is larger than other comparisons between predicted and observed bill depths of crossbill populations specialized on other conifers in western North America (Benkman 1993; Benkman et al. 2001).

One hypothesis for this discrepancy is that an ectoparasite, the scaly-leg mite (*Knemidokoptes jamaicensis*), differentially infects large-billed South Hills crossbills, causing directional selection for smaller bill depths (Benkman et al. 2001, 2003; Benkman 2003). Birds infected with scaly-leg mites are characterized by crusty lesions on their legs and feet resulting from the burrowing of mites into epithelial layers (Turk 1950). This can cause loss of digits and feet (Pence et al. 1999), and some evidence suggests that infections are often lethal (Latta and Faaborg 2001; Latta 2003); birds presumably cannot physically remove these mites once infected. The goals of our study were to document the incidence of scaly-leg mites and employ more sophisticated capture-recapture models (via MARK) to determine if annual survival (ϕ_i) varied with bill depth, sex, and the occurrence of mites. We considered sex in the analyses because preliminary results indicated that male crossbills were more likely to show symptoms of scaly-leg mites than were females: Many studies report sex-biases (usually a male-bias) in the occurrence and severity of parasites (e.g., Moore and Wilson 2002). Although

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South Hills crossbills are the first documented to exhibit scaly-leg mite infestations, populations in the Netherlands have recently been found to exhibit symptoms of scaly-leg mites (P. Edelaar, pers. comm.) and in 2004 symptoms of scaly-leg mites were observed on red crossbills in the Black Hills, South Dakota (C. W. Benkman, pers. obs.). This suggests that crossbills are either a recent host of scaly-leg mites or that scaly-leg mites were previously rare in crossbills. Indeed, the crossbill population coevolving with lodgepole pine in the Cypress Hills may have matched the predicted foraging optimum because scaly-leg mites were absent when specimens were collected in 1930–1940; the Cypress Hills crossbill is likely extinct because of the introduction of pine squirrels (*Tamiasciurus hudsonicus*) in 1950 (Benkman 1999).

Crossbills represent an excellent system in which to examine selection because of the direct functional link between morphology, performance, ecology, and survival of crossbills (Benkman 1993, 2003; Benkman et al. 2001, 2003). South Hills crossbills are an especially tractable system because they are resident within 100 km² of lodgepole pine forest in southern Idaho (Benkman 1999, 2003; Benkman et al. 2001, 2003). Moreover, they eat almost exclusively seeds in lodgepole pine cones, whose annual seed crops are exceptionally stable (T. Fetz and C. W. Benkman, unpubl. data; Benkman et al. 2003), so that ecologically based selection should be similar among years. Bill depth, which has been the focal morphological trait in our research (e.g., Benkman 1993, 2003), is generally highly heritable in birds (Merilä and Sheldon 2001), including crossbills ($h^2 \approx 0.7$, R. Summers, pers. comm.) and should respond to selection. Finally, South Hills crossbills possess a distinctive flight call (Benkman 1999) that distinguishes them from three other crossbill call types (Groth 1993) that frequent the South Hills (J. W. Smith, T. Fetz, C. W. Benkman, unpubl. data).

MATERIALS AND METHODS

Incidence of Scaly-leg Mites and Bill Depths of South Hills Crossbills

Crossbills were captured during the summers between 1997 and 2004 in the South Hills, Idaho. Capture effort took place in two general areas approximately 8 km apart: Porcupine Springs (42°10'6.8"N, 114°15'52.5"W) and Bostetter (42°10'16"N, 114°9'56.3"W). One to three 12-m nylon mist nets were set up between 0600 and 1300 h near where crossbills often flew to the ground for water, charcoal, or salts. In addition, two or more live South Hills crossbills were held in cages as lures and placed near nets. Crossbills were captured on 231 days: 26–30 July 1997 (5 days); 8 July–4 August 1998 (21 days); 26–28 July 1999 (3 days); 10–21 July 2000 (12 days); 21–23 June and 1–10 August 2001 (12 days); 11 June–6 August 2002 (50 days); 20 May–28 July 2003 (50 days); and 26 May–24 August and 25–27 September 2004 (78 days).

Upon capture, crossbills were aged, sexed, and visually examined for presence or absence of the symptoms of scaly-leg mite infestation (hereafter, mites). Hatch-year birds (juvenile and immature) were recognized by the heavy brown streaking on their undersides; crossbills breed in spring and

summer in the South Hills. Adult crossbills (after-hatch-year) were sexed by the color of their contour feathers: males are red, orange, or bright yellow (including their throat feathers), whereas females are greenish (with grayish throat feathers). Crossbills with smooth black tarsi were considered free of mites, whereas crossbills with scaly, whitish gray, swollen tarsi were considered infected with mites. Mites were identified to morphological species from scrapings of the legs of two crossbills that had scaly, whitish gray, swollen tarsi (D. Pence, pers. comm.). Only adults showed evidence of mite infestation. Crossbills were categorized for presence/absence of mites at the time of their initial capture as an adult; six of 60 adult crossbills initially captured without mites had mites at a later capture date.

Crossbills were banded with uniquely numbered U.S. Fish and Wildlife Service (USFWS) aluminum bands to allow individual identification. In 1998, we began placing plastic color bands on the tarsus opposite of the USFWS band. Only adults were color-banded because of limited color combinations and because banded hatch-year crossbills were much less likely to be seen in subsequent years than were those banded as adults (e.g., only eight of 106 [7.6%] hatch-year birds banded in 2002 were recaptured in 2003). We did not band crossbills with mites until 2002, because we were concerned that the bands would aggravate the tarsi (e.g., Kirmse 1966) and because some of the tarsi were so swollen there would have been little if any space for the band to move freely along the tarsus. In 2002, however, we began to uniquely mark adult crossbills that had mites with larger sized and loosely fitting colored plastic bands.

Bill depth was measured for nearly all captured crossbills. Digital calipers were used to measure bill depth three to five times per bird to the nearest 0.01 mm at the anterior edge of the nares (Benkman 1993); we used the mean of the measurements in analyses or the mean of means for recaptured crossbills. Four researchers have measured crossbills in the South Hills since 1997: C.W. Benkman in all years, W. C. Holimon in 1998, J. S. Colquitt in 2002 and 2003, and P. Keenan in 2004. When we were able to compare measurements made on the same crossbills but on different capture occasions, our measurements were generally similar and highly repeatable (Lessells and Boag 1987). Bill depth measurements of 17 crossbills made about a month apart by Benkman and Holimon were nearly identical (mean difference was 0.001 mm) and repeatable (repeatability = 0.892, $F_{1,16} = 16.1$, $P = 0.001$). Likewise, bill depth measurements of 21 crossbills made by Colquitt one or more years after Benkman measured them were also very similar (mean difference was 0.005 mm) and highly repeatable (repeatability = 0.997, $F_{1,20} = 31.3$, $P < 0.001$). The repeatability of 47 crossbills recaptured and remeasured two or more times within a year by Colquitt was also very high (repeatability = 0.989, $F_{3,46} = 43.6$, $P < 0.001$). However, the 18 crossbills remeasured by Colquitt in 2003 were on average 0.068 mm larger than in 2002. The repeatability of bill depth measurements between these two years was also lower (repeatability = 0.497, $F_{1,17} = 17.8$, $P < 0.001$). Consequently, we used the mean of previous measurements for crossbills recaptured in 2003 but did not correct the bill depth measurements made of crossbills initially captured in 2003. One possible explanation for the

difference in bill depths between years is that bill depth continues to grow in crossbills who are two or more years old. Such growth, however, is not consistent with the similarity in average bill depths between those measured by Benkman and Colquitt in different years, nor is it consistent with the nearly identical average bill depths of second-year and after-second-year males (9.94 mm and 9.95 mm, respectively; t -test, $t_{117} = 0.28$, $P = 0.78$) and females (9.76 mm and 9.77 mm, respectively; t -test, $t_{68} = 0.15$, $P = 0.88$). Most of the crossbills captured in 2004 were measured by P. Keenan, whose estimates of repeatability between captures and between his measurements and those made by others was very low, thus only the resighting and recapture data from 2004 were used in our analyses, allowing better estimates of survival for birds with mites banded in 2002 and 2003.

A Marantz (Aurora, IL) PMD-222 tape recorder and a Sennheiser (Old Lyme, CT) directional microphone were used to record the flight calls of crossbills upon release. Individual flight-call analyses were made using Canary software (Cornell Laboratory of Ornithology, Ithaca, NY) on a Macintosh computer. Not all crossbills called, nor could all calls be classified to call type (89 of 784 [11.4%] adult crossbills could not be classified to call type; many crossbills are stressed upon capture and some do not call or give their normal flight call upon release). All analyses were based on individuals that were identified as adult South Hills crossbills, which represented 91% (634 of 695) of the captured and classified adult crossbills in the South Hills.

Logistic regression and Wald chi-square statistics were used to determine if the incidence of mites varied in relation to year of capture and sex, and t -tests were used to determine if birds with and without mites differed in bill depth. Least-squares linear regressions were used to determine if bill depth varied linearly across years. Individuals were not used more than once for a given year, but we included recaptures in the analyses comparing the incidence of mites and bill depth among years; recaptures represented only 8% of the individuals used in these analyses. Because we did not band crossbills with mites prior to 2002, some crossbills with mites could have been counted more than once. This is unlikely, however, because recaptures were uncommon prior to 2002 due to limited sampling intensity and crossbills with mites had relatively low survivorship (see Results).

Estimation of Annual Survivorship and Model Selection Using MARK

The Cormack-Jolly-Seber (CJS) model (Cormack 1964; Jolly 1965; Seber 1965) was used to estimate survival based on live capture/resighting data from 1998 to 2004. Individuals captured in 1997 and 1999 were excluded because individuals were not uniquely color-banded. In addition to the netting effort previously described, banded crossbills were resighted with telescopes (40× Questar [New Hope, PA] and 20–60× Kowa [Tokyo] scopes) between 2000 and 2004 for approximately two or more weeks in each of the following months: July, October, and December 2000; June through December 2001 and 2002; March through August 2003; and March through July and September 2004.

Parameter estimation and model selection was done using

MARK (White and Burnham 1999). The first step was to construct a fully parameterized general model that allowed for time variation in capture probabilities and survival rates for four different groups: males without mites, males with mites, females without mites, and females with mites. However, the dataset proved too sparse for such a heavily parameterized model. Thus, the most general model from which reasonable submodels could be evaluated was one that allowed group-specific survival rates (ϕ_{group}) and capture probabilities to vary over time by sex. Because of a lack of resighting effort in 1999, capture probability for this occasion was constrained to zero (resulting in one fewer estimated parameter). Even though our recapture/resighting effort extended over several months each year, we treated all recaptures and resightings within a given year as if they occurred at the same time.

Models were considered both with and without the covariate bill depth. To facilitate numerical convergence in MARK, bill depth for each individual was scaled down by a factor of 10 (Franklin 2001). Survival was modeled as a logistic function of bill depth using the logit link function such that,

$$\text{logit}(\phi_i) = \hat{\beta}_0 + \hat{\beta}_1(\text{bill}) + \hat{\beta}_2(\text{bill})^2 \quad \text{or} \quad (1a)$$

$$\phi_i = \frac{1}{1 + \exp\{-[\hat{\beta}_0 + \hat{\beta}_1(\text{bill}) + \hat{\beta}_2(\text{bill})^2]\}} \quad (1b)$$

Nested versions of the survival function, so that $\hat{\beta}_2$ was constrained to zero, were also examined. In the analyses, the above stated four groups were allowed differing intercepts and slopes initially (interactive model) and subsequently were examined for a common slope and a common intercept. Akaike's information criterion values (AIC_c) were used to rank the models, where the lowest AIC_c represented the best model. Because we were exploring possible evolutionary processes, it is reasonable to consider models close to the lowest AIC_c model. Models were considered well substantiated if their AIC_c differed by <2 ($\Delta_i < 2$) from the best model (Akaike 1992). If their AIC_c differed by >2 but by <4 , they were considered less well substantiated but nevertheless informative (Akaike 1992). Relative likelihood of each model in a candidate set was estimated with AIC_c weights (w_i ; Burnham and Anderson 1998), which sum to one in a candidate set. A total of 235 crossbills without mites and 82 crossbills with mites were included in the analyses using MARK. Unfortunately, the time intervals for estimating survival for birds with and without mites were not completely coincident (2002–2004 and 1998–2004, respectively). Nevertheless, most (65%) of the birds without mites used in the survival analyses were banded after 2001, so that the estimates of survival for the two groups were based largely on the same time period.

RESULTS

Incidence of Mites from 1997 to 2004

Incidence of mites varied among years (logistic regression: $\chi^2 = 19.66$, $P = 0.006$) and in relation to sex ($\chi^2 = 7.38$, $P = 0.007$) with the interaction between time and sex not detectable ($\chi^2 = 7.50$, $P = 0.38$; Fig. 1). The incidence of mites

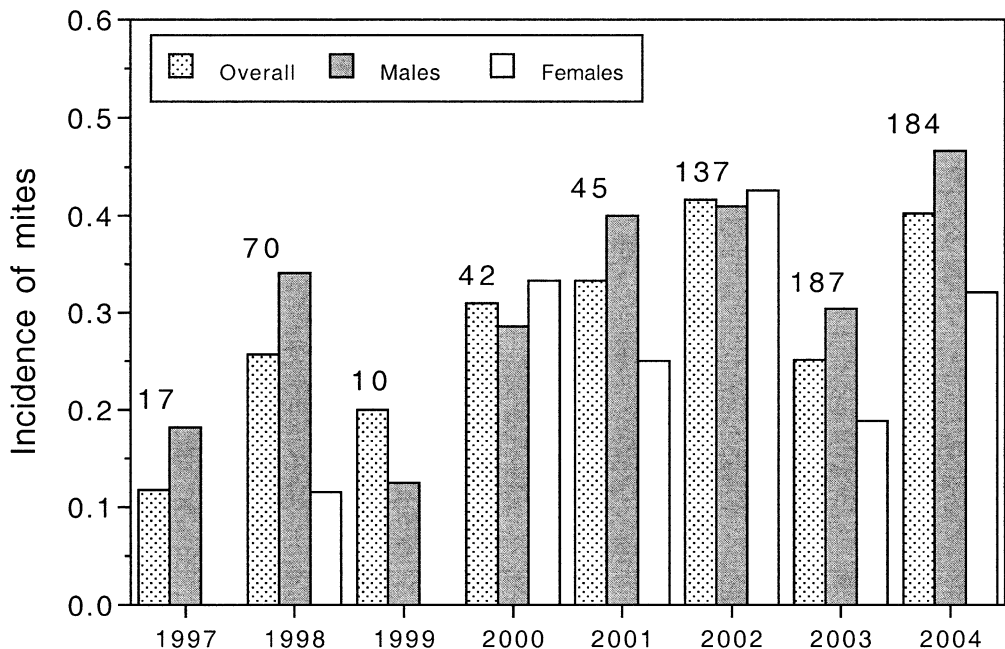


FIG. 1. The incidence of mites among adult South Hills crossbills (unweighted by sex; sample sizes above bars), adult males, and adult females from 1997 to 2004. In 1997, none of the six females had evidence of mites. In 1999, one of two females had mites but this is not shown.

reached a peak incidence of 41.6% in 2002, then declined in 2003, and returned to an incidence of 40.2% in 2004. The overall incidence of mites was 37.0% for males and 27.5% for females (Fig. 1).

Incidence of Mites in Relation to Bill Depth

Males with mites had significantly larger bills than males without mites (with mites: 10.02 mm, SE = 0.02, $n = 97$ birds; without mites: 9.94 mm, SE = 0.03, $n = 172$; t -test: $t_{267} = 2.32$, $P = 0.021$). The incidence of mites in females was unrelated to bill depth (with mites: 9.72 mm, SE = 0.04, $n = 46$ birds; without mites: 9.74 mm, SE = 0.03, $n = 145$; t -test: $t_{192} = 0.39$, $P = 0.70$).

Survival in Relation to Presence of Mites, Sex, and Bill Depth

Three of the top four models for adult annual survival included the presence/absence of mites (ϕ_{mite} ; Table 1) and treated capture probabilities as time dependent (p_{t-1} ; the probability of recapture in 1999 set at zero). The lowest-AIC_c model (model 1 in Table 1) revealed that adult survival with mites (0.626) was 15% lower than for those without mites (0.735; Table 2). When ϕ was parameterized by sex and presence/absence mites (model 9 in Table 1), males without mites tended to have a higher annual survivorship than females without mites (male survivorship = 0.754 ± 0.044 ; female survivorship = 0.716 ± 0.045). This contrasts with

TABLE 1. Models of annual survival (ϕ) and capture (p) probabilities for South Hills crossbills, number of estimable parameters (K), Akaike's information criterion values (AIC_c), AIC_c differences (Δ_i), and AIC_c weights (w_i). Subscripts give parameterizations for ϕ and p : (.), constant over group and time variables; mite, mites present or absent; bill and bill², linear and quadratic logistic functions, respectively, of bill depth; sex, male and female; $t - 1$, recapture probabilities were set at zero for 1999 and the rest of the years were estimated (see Table 2); asterisk, an interaction allowing for differing slopes as well as different intercepts; plus symbol, at least one common parameter in the logistic function.

Model	K	AIC _c	Δ_i	w_i
(1) $\phi_{\text{mite}}, p_{t-1}$	7	690.95	0.00	0.19
(2) $\phi(\cdot), p_{t-1}$	6	691.01	0.06	0.19
(3) $\phi_{\text{mite+bill}}(\text{same intercept}), p_{t-1}$	8	692.05	1.10	0.11
(4) $\phi_{\text{mite+bill}}(\text{same slope}), p_{t-1}$	8	692.10	1.15	0.11
(5) $\phi_{\text{bill}}, p_{t-1}$	7	692.26	1.31	0.10
(6) $\phi_{\text{sex}}, p_{t-1}$	7	692.98	2.03	0.07
(7) $\phi_{\text{mite+bill}^2}(\text{same slope}), p_{t-1}$	9	693.24	2.29	0.06
(8) $\phi_{\text{mite*bill}}, p_{t-1}$	9	693.85	2.90	0.05
(9) $\phi_{\text{mite*sex}}, p_{t-1}$	9	694.26	3.31	0.04
(10) $\phi_{\text{mite+bill}^2}(\text{same intercept}), p_{t-1}$	10	694.94	3.99	0.03
(11) $\phi_{\text{mite*sex+bill}}(\text{different intercept}), p_{t-1}$	10	694.98	4.03	0.03
(12) $\phi(t), p_{t-1}$	10	695.28	4.33	0.02
(13) $\phi_{\text{mite*sex*bill}}, p_{t-1}$	13	700.21	9.26	0.00
(14) $\phi_{\text{mite*sex}}, p_{\text{sex}*t-1}$	14	701.20	10.26	0.00

TABLE 2. Estimated survival for all years (ϕ) and probabilities of recapture/resighting given that the bird was alive for each year of study (p) with standard errors (SE) and lower and upper 95% confidence intervals for model 1 in Table 1.

Parameter	Estimate	SE	Lower	Upper
ϕ (mite)	0.626	0.075	0.472	0.758
ϕ (miteless)	0.735	0.034	0.664	0.795
p (1999, fixed)	0.000	0.000	0.000	0.000
p (2000)	0.424	0.131	0.206	0.678
p (2001)	0.579	0.109	0.364	0.767
p (2002)	0.879	0.055	0.724	0.953
p (2003)	0.870	0.058	0.710	0.948
p (2004)	0.422	0.051	0.327	0.522

the relative survivorship of the two sexes when infected with mites (male survivorship = 0.592 ± 0.094 ; female survivorship = 0.679 ± 0.112), and indicates that mites reversed the relative survivorship of the two sexes and depressed male survivorship more than they depressed female survivorship.

Many of the best models ($\Delta_i < 4$) included bill depth as a covariate of survival (Table 1). When a common slope was assumed for birds with and without mites (model 4 in Table 1), survivorship decreased with increasing bill depth (Fig.

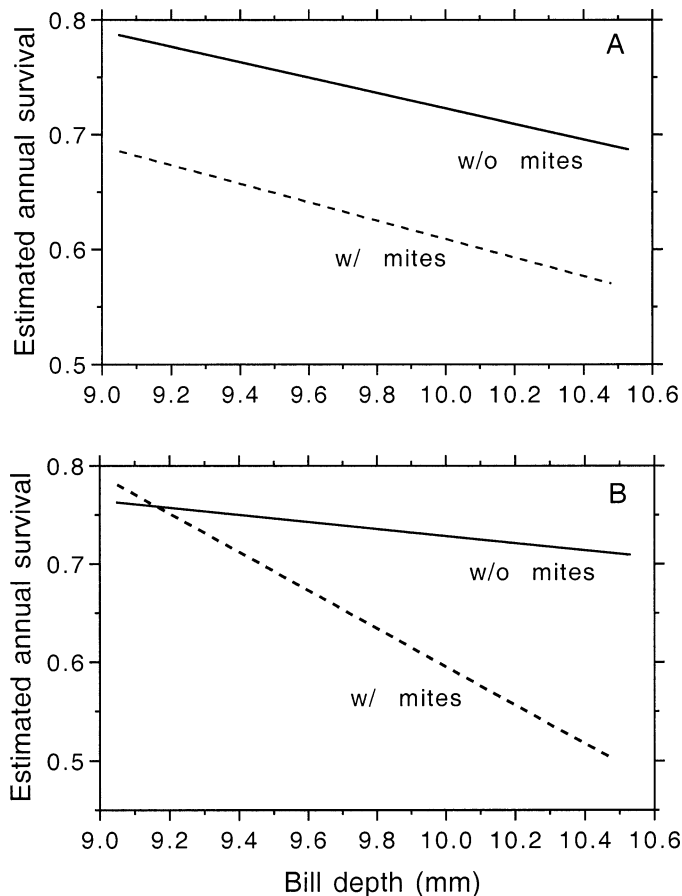


FIG. 2. Estimated annual survival in relation to bill depth based on capture/recapture models for (A) a common slope between crossbills with and without mites (model 4 in Table 1) and (B) where the slopes and intercepts were allowed to vary independently between crossbills with and without mites (model 8 in Table 1).

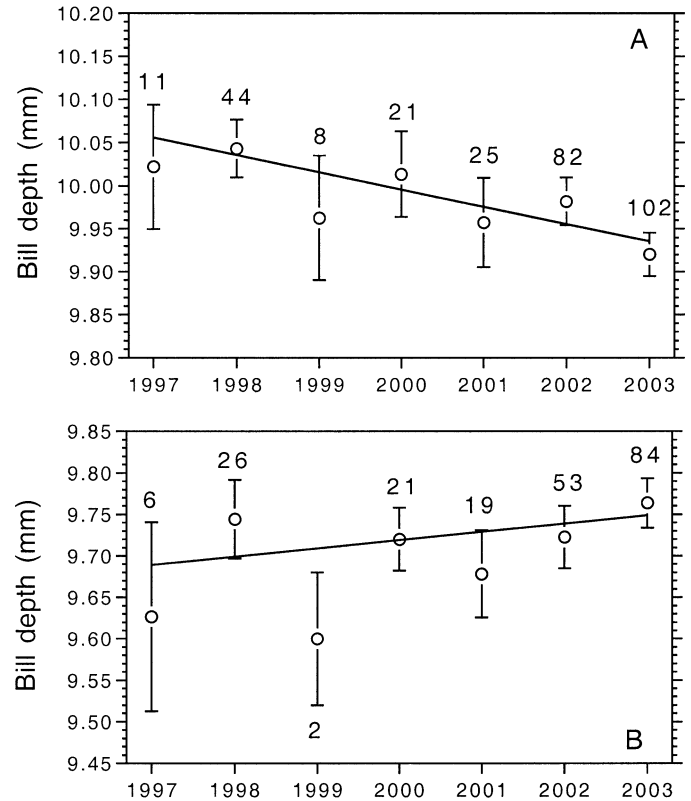


FIG. 3. Mean bill depth (\pm SE) decreased for males (A) but not females (B) from 1997 to 2003. The solid lines represent the linear regressions using measurements of all individuals ($n = 293$ males and 211 females), including between-year recaptures.

2A); the result for the model with a common intercept (model 3 in Table 1) was nearly identical (not shown). Models including a quadratic effect for bill depth did not provide a better fit than the models with a linear effect (e.g., likelihood-ratio test comparing model 7 to model 4: $\chi^2 = 0.94$, $P = 0.33$). When the model allowed the slopes as well as the intercepts to differ between birds with and without mites (model 8 in Table 1), survivorship decreased much more markedly with increases in bill depth for birds with mites than for those without mites (Fig. 2B). We interpret the results in Figure 2B to most accurately represent survival relationships between birds with and without mites and bill depth, because it is a more flexible model that is reasonably well supported according to AIC_c criterion (Table 1). These results show that mites adversely affected survivorship and that larger-billed crossbills were the most affected. This leads to selection against larger-billed crossbills; the standardized selection gradient (β ; Lande and Arnold 1983) on bill depth for birds with mites (Fig. 2B) was -0.084 . Larger-billed males were at a further disadvantage because they were also more likely to have mites.

Are Bill Depths Getting Smaller?

Bill depths for males (with and without mites) decreased linearly from 1997 to 2003 (Fig. 3A; $F_{1,291} = 7.27$, $P = 0.007$), whereas there was no evidence for a linear change in bill depth for females over time (Fig. 3B; $F_{1,209} = 1.07$,

$P = 0.30$). Mean bill depth for males decreased 0.12 mm from 1998 (10.04 mm, SE = 0.03) to 2003 (9.92 mm, SE = 0.03; t -test: $t_{144} = 2.75$, $P = 0.0067$). As a result, the difference between the mean bill depth of males and females decreased by nearly a half, from 0.30 mm in 1998 to only 0.16 mm in 2003. Similarly, sexual size dimorphism in bill depth decreased from males being 3.1% larger to only 1.6% larger. This decrease in bill depth for males is equal to a phenotypic change of 0.149 haldanes (change in standard deviations per generation; Hendry and Kinnison 1999), assuming a generation time of 2.9 years for males (estimated by the life table method [Krebs 2001] assuming $\lambda = 1$ and an average annual adult survivorship of 0.7 based on the survivorship and incidence of mites in males). This measure of phenotypic change (0.149 haldanes) is in the range of values found in previous studies of microevolution for such a short time period (Hendry and Kinnison 1999), but greater than the median value (0.035) for studies covering fewer than 80 generations (Kinnison and Hendry 2001).

DISCUSSION

Bill depths of male but not female South Hills crossbills decreased by 0.12 mm from 1998 to 2003, apparently because males, especially those with large bills, were more likely to have mites and crossbills with mites were less likely to survive as bill size increased. Although we doubt bill depth is the target of selection by mites, bill depth is under selection because it is strongly correlated with body size (Benkman 2003), which is likely more closely related to the target of selection. Such directional selection on males for smaller bill size can also explain, at least in part, why the average bill depth of South Hills crossbills in 2003 (9.84 mm, weighted by sex; $n = 186$ crossbills) was 0.15 mm smaller than the optimum for foraging on lodgepole pine cones in the South Hills (predicted optimum is 9.99 mm; Benkman et al. 2001). In addition, directional selection on males, but not on females, has reduced the extent of sexual size dimorphism in bill depth in this population by half in five years; because body mass is allometrically related to bill depth in red crossbills, there should be a corresponding decrease in sexual dimorphism in body size (Benkman 2003). Before discussing further the various results of this study, we address the assumptions of the CJS model.

Assumptions of Cormack-Jolly-Seber Model

One assumption of the CJS model is that all emigration is permanent or that if temporary emigration exists, it is random with respect to marks. Some crossbills do move within the South Hills. For example, we netted crossbills in two general areas 8 km apart, and five of 208 (2.4%) adult crossbills that we resighted or recaptured moved between these two areas. Nevertheless, we suspect limited movement within or out of the South Hills because the food resource (seeds in conifer cones) is so stable (Benkman et al. 2003). If emigration is permanent, estimated survival would be underestimated. However, we are unable to identify a reason for this bias to affect mite and nonmite birds differently.

We also assumed that our recapture and resighting interval was brief, yet it took place over several months each year.

Although this can cause bias in estimates of annual survival, recent work indicates that the bias is minimal provided the pattern of initial captures within survey periods is not vastly different among years (P. Conn, pers. comm.). The assumption that survival for marked birds is equal to unmarked birds is reasonable given that birds are only being banded (as opposed to fitted with radio telemetry devices) and that handling times are kept to a minimum. Heterogeneity of capture probabilities is likely to exist to some extent, but its presence has minimal effect on estimated survival. Finally, 10% of the crossbills initially captured without symptoms of mites later acquired mites. Thus, our estimates of survival for birds without mites, which refers only to their condition at initial capture, will tend to underestimate survival for crossbills that never developed symptoms of mites. Such a bias, particularly if large-billed birds are more likely to acquire and die from mites than small-billed birds, may underlie the slight decrease in survival as bill depth increases for birds initially captured without mites (Fig. 2B). Alternatively, some unknown agent in the environment may have caused selection against larger billed crossbills and those with mites were disproportionately affected.

Variation in the Incidence of Mites

Over 28% of male South Hills crossbills had mites since 1997, with the exception of 1999, when only one of the eight males captured had mites. The incidence of mites in males was also relatively low in 1997, when the sample size was small (Fig. 1). In contrast, the incidence of mites on females tended to increase until 2002, decline in 2003, and then return to a higher incidence in 2004 (Fig. 1). The increase and fluctuations in mites may simply reflect the dynamics of an epidemic. Other studies have found higher incidences of mites in warmer, more arid environments (Latta and Faaborg 2001; Latta 2003). Although the climate in the South Hills has become increasingly warm and dry over the past six years (C. Chaffin, pers. comm.), the decrease in mite prevalence in 2003 occurred during the warmest and driest year.

The higher incidence of mites in male than female South Hills crossbills is consistent with interspecific comparisons among mammals, which show that parasitism becomes increasingly male biased as sexual size dimorphism increases (Moore and Wilson 2002). Crossbills are sexually size dimorphic with males larger than females; body masses of males are larger than those of females by 2.1% in South Hills crossbills (based on 60 males and 27 females captured in 2003 and 2004 without noticeable fat) and on average by 4.1% among six taxa of North American red crossbills (data in Groth 1993). We suspect that the relatively low level of sexual size dimorphism in South Hills crossbills compared to other red crossbills is related to recent selection exerted by mites. Several explanations are possible for a higher incidence of mites in males with increasing sexual size dimorphism (Moore and Wilson 2002). Mites may have been more frequent in males than females if mites are transmitted more readily between males, if males are more susceptible to infections by mites, or both. Unfortunately, no information is available on the transmission of mites between hosts; however, transmission likely increases with direct contact (Wich-

man and Vincent 1958). Because male crossbills tend to have higher rates of agonistic interactions, which can include direct contact (Benkman 1997), they may experience higher transmission rates.

Male crossbills may be more susceptible to the detrimental effects of mites because they have higher levels of androgens, such as testosterone, than females, and higher levels of androgens compromise the immune system in some birds and mammals (Folstad and Karter 1992; Duffy et al. 2000; Evans et al. 2000; Peters 2000; Castro et al. 2001; Duckworth et al. 2001; Mougeot et al. 2004). This might also account for the higher incidences of mites in large-billed males than small-billed males, because dominant individuals tend to be larger (Lahti 1998), as found in two other species of cardueline finches (Björklund 1989; Senar et al. 2000), and have higher levels of testosterone than do subordinates (Ramenofsky 1984; Wingfield 1985; Hegner and Wingfield 1987; Duckworth et al. 2001; but see Belthoff et al. 1994).

Survival in Relation to Bill Depth

The higher incidence of mites in males (Fig. 1) combined with both a bias for larger-billed males to express symptoms of mite infection and size-biased survival among those with these symptoms (Fig. 2) results in directional selection favoring individuals with smaller bills especially among males. In addition to being consistent with interspecific comparisons among mammals (Moore and Wilson 2002), our results are also consistent with a study on another species of cardueline finch (*Carpodacus mexicanus*) during an epidemic of *Mycoplasma gallicepticum* (Nolan et al. 1998) that showed males, and apparently large males, may have suffered disproportionately high mortality.

The result of these factors is directional selection against larger billed (and bodied) male crossbills in the South Hills that presumably counters sexual selection favoring larger males. This suggests that selection by parasites has the potential to limit the extent of sexual size dimorphism. However, why female bill depth did not decrease as a correlated trait is less certain (e.g., Lande 1980). If mites differentially affect males over females and especially larger-billed (-bodied) males because of elevated levels of testosterone, then an evolutionary response could be a lowering of testosterone production. Thus, if testosterone affects male but not female size, then a decline in male but not female size is expected. In addition, because females tend to have bill depths that are smaller than the foraging optimum, there may have been strong selection against decreases in bill size in females.

Finally, survival varied little with bill depth among crossbills without evidence of mites (Fig. 2B). This contrasts with evidence in an earlier study (Benkman 2003) that indicated selection was stabilizing on bill depth among crossbills without mites. Those data were mostly from crossbills banded as adults in 1998 and perhaps reflect selection before mites had increased to their highest levels. Presumably, as mortality increased from mites, food became less limiting for adults without mites and density-dependent processes and selection in relation to feeding efficiency decreased. Conversely, if mites decrease in the future, then food should become more limiting and selection should once again favor crossbills with

the optimum bill depth for feeding on lodgepole pine cones in the South Hills (see Benkman et al. 2001; Benkman 2003). This would lead to directional selection on South Hills crossbills favoring a larger bill depth, because on average their bill depth is 0.15 mm less than the predicted optimum.

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