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AN EVALUATION OF LONG-TERM CAPTURE EFFECTS IN URSIDS: IMPLICATIONS FOR WILDLIFE WELFARE AND RESEARCH

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The need to capture wild animals for conservation, research, and management is well justified, but long-term effects of capture and handling remain unclear. We analyzed standard types of data collected from 127 grizzly bears (*Ursus arctos*) captured 239 times in western Alberta, Canada, 1999–2005, and 213 American black bears (*U. americanus*) captured 363 times in southwestern North Carolina, 1981–2002, to determine if we could detect long-term effects of capture and handling, that is, effects persisting $\geq$1 month. We measured blood serum levels of aspartate aminotransferase (AST), creatine kinase (CK), and myoglobin to assess muscle injury in association with different methods of capture. Serum concentrations of AST and CK were above normal in a higher proportion of captures by leghold snare (64% of 119 grizzly bear captures and 66% of 165 black bear captures) than capture by helicopter darting (18% of 87 grizzly bear captures) or by barrel trap (14% of 7 grizzly bear captures and 29% of 7 black bear captures). Extreme AST values (>5 times upper reference limit) in 7 (6%) grizzly bears and 29 (18%) black bears captured by leghold snare were consistent with the occurrence of exertional (capture) myopathy. We calculated daily movement rates for 91 radiocollared grizzly bears and 128 radiocollared black bears to determine if our activities affected their mobility during a 100-day period after capture. In both species, movement rates decreased below mean normal rate immediately after capture (grizzly bears: $\bar{X}$ = 57% of normal, 95% confidence interval = 45–74%; black bears: 77%, 64–88%) and then returned to normal in 3–6 weeks (grizzly bears: 28 days, 20–37 days; black bears: 36 days, 19–53 days). We examined the effect of repeated captures on age-related changes in body condition of 127 grizzly bears and 207 black bears and found in both species that age-specific body condition of bears captured $\geq$2 times (42 grizzly bears and 98 black bears) tended to be poorer than that of bears captured once only (85 grizzly bears and 109 black bears), with the magnitude of effect directly proportional to number of times captured and the effect more evident with age. Importantly, the condition of bears did not affect their probability of capture or recapture. These findings challenge persons engaged in wildlife capture to examine their capture procedures and research results carefully. Significant capture-related effects may go undetected, providing a false sense of the welfare of released animals. Further, failure to recognize and account for long-term effects of capture and handling on research results can potentially lead to erroneous interpretations.

Key words: American black bear, body condition, exertional myopathy, grizzly bear, long-term capture effects, movement rates, muscle injury, ursids, *Ursus americanus*, *Ursus arctos*

Information gathered from wild animals is required for wildlife research, conservation, and management. Although much can be learned by indirect techniques, such as collecting fecal samples to determine hormone status (Foley et al. 2001; Millspaugh et al. 2001) or collecting hair for DNA analysis (Beier et al. 2005; Boulanger et al. 2004), some information is collected only by capturing animals, for example, age determination, morphometric measurements, or serum biochemistry (Garshelis 2006; Powell and Proulx 2003). Capture of wild animals has potential to cause injury and to change

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normal behavior and physiology (Kreeger et al. 1990; Proulx 1999). Consequently, researchers are challenged to design research and use methods that have minimal impact on study animals and remain safe for field personnel. Procedures that affect study animals adversely not only raise important ethical and animal welfare issues but also are likely to influence the animals' behavior or physiology in ways that affect research results (Powell and Proulx 2003).

A major obstacle to gathering information on effects of capture and handling, especially those occurring over periods of weeks or months, is that these effects can be difficult to detect. Mortality rates are sometimes used to evaluate capture procedures (Arnemo et al. 2006; DelGiudice et al. 2005; Haulton et al. 2001). Observed mortality rates, however, may not provide accurate estimates of true mortality rates unless survival of all released animals is confirmed for an adequate period after capture (Lebreton et al. 1992; Schaub and Pradel 2004). Mortality may go undetected because, for example, scavengers or predators consume carcasses, animals die in concealed places, carcasses decompose quickly, radiotransmitters malfunction, or animals fitted with radiotransmitters emigrate from the study area (Bunck et al. 1995; Vyas 1999; Wobeser and Wobeser 1992). More importantly, mortality rates provide no information on how many animals might be negatively affected by capture short of death.

The full impact of capture and handling procedures cannot be determined without evaluating physical, behavioral, and physiological effects on captured animals at the time of capture and in the days and weeks that follow. Perhaps because assessment of all potential effects over different timescales is difficult to carry out, comprehensive reports covering capture effects over wide timescales are few (an exception is the series of publications by Kock et al. [1987a, 1978b, 1987c]). Researchers more often report only the short- or intermediate-term effects of capture and handling, such as physical injury (e.g., Peterson et al. 2003; Shivik et al. 2005) or significant changes in blood and other physiological values (e.g., Golden et al. 2002; Marco et al. 1997; Storms et al. 2005) that persist from minutes to days. Although documentation of long-term effects is sparse, several recent publications conclude that capture and handling may have significant consequences not only for specific wild populations (Alibhai et al. 2001; Côté et al. 1998) but also for the accuracy and interpretation of research results (Clinchy et al. 2001). However, other studies have not found convincing evidence for long-term adverse effects (Creel et al. 1997; Laurenson and Caro 1994; Lunn et al. 2004).

Herein, we report on an evaluation of long-term ($\geq$1-month) effects of capture and handling in 2 ursid species, grizzly bears (*Ursus arctos*) and American black bears (*U. americanus*). Our data originate from 2 independent studies, the Foothills Model Forest Grizzly Bear Research Project and the Pisgah Bear Sanctuary Black Bear Research Project, conducted by different teams of researchers in geographically distinct areas. Prompted by findings from previous studies (Cattet et al. 2003b; Powell 2005), we resolved to evaluate whether long-term effects of capture and handling were detectable and, if so, to determine what possible implications this could have for the welfare of released animals and the interpretation of research results. Our analysis was entirely retrospective and, unless stated otherwise, we use the phrase ''capture and handling'' in the broadest sense to include the combination of all procedures, that is, pursuit or restraint, anesthesia, tooth extraction, application of radiotelemetry equipment, and so on. Our primary objectives were to document occurrence and severity of capture-related muscle injury, to evaluate the mobility of bears in the weeks after capture, and to determine if body condition of bears was affected by repeated captures.

Materials and Methods

Foothills Model Forest Grizzly Bear Research Project.—We captured 127 grizzly bears 239 times between April 1999 and August 2005 (research goals are summarized by Stenhouse and Graham [2005]) within a 150,000-km^2 area of western Alberta, Canada (49°00′–55°50′N, 113°50′–120°00′W). Captured bears were composed of 61 females (1–21 years old at 1st capture) and 66 males (1–19 years old at 1st capture). Females included 25 juvenile ($<$5 years old) and 36 adult bears ($\geq$5 years old), whereas males included 32 juveniles and 34 adults.

We used Aldrich leghold snares (Aldrich Snare Co., Clallam Bay, Washington) for 130 captures, remote drug delivery from helicopter (helicopter darting) for 99 captures, and barrel traps for 10 captures (Cattet et al. 2003b). All bears were anesthetized by remote drug delivery (Pneu-Dart Inc., Williamsport, Pennsylvania, and Paxarms NZ Ltd., Timaru, New Zealand) using a combination of xylazine and zolazepam–tiletamine administered intramuscularly as xylazine (Cervizine 300; Wildlife Pharmaceuticals, Inc., Fort Collins, Colorado) at 2 mg/kg and Telazol (Fort Dodge Laboratories, Inc., Fort Dodge, Iowa) at 3 mg/kg estimated body weight (Cattet et al. 2003a). We administered atipamezole (Antisedan; Novartis Animal Health Canada Inc., Mississauga, Ontario, Canada) at 0.15–0.20 mg/kg, half-volume intramuscularly and half-volume intravenously, to reverse the effects of xylazine.

We recorded pulse and respiratory rates, rectal temperature, and hemoglobin oxygen saturation (Nellcor NPB-40 pulse oximeter; Nellcor, Pleasanton, California) for all bears at onset of handling and every 15 min thereafter during a $\leq$75-min handling period. We extracted a premolar tooth to estimate age by counting cementum annuli (Stoneberg and Jonkel 1966). We weighed bears in a sling suspended beneath a load scale (MSI-7200 Dynalink; Precision Giant Systems Inc., Edmonton, Alberta, Canada) and measured body length as dorsal straight-line distance from tip of nose to end of last tail vertebra.

We collected blood from the femoral vein into sterile tubes for biochemical analysis, and into an ethylenediaminetetraacetic acid tube for measurement of complete blood count. We centrifuged blood samples within 8 h of collection, and extracted and froze (−20°C) serum for biochemistry analysis using an Abbott Spectrum Series II biochemistry analyzer (Abbott Laboratories Diagnostic Division, Abbott Park, Illinois), and for myoglobin analysis using an ADVIA Centaur immunoassay system (Bayer Healthcare, Tarrytown, New York). We chilled blood samples in ethylenediaminetetraacetic

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acid for determination of complete blood cell counts within 24 h of collection using an Abbott Cell-Dynn 3200 hematology analyzer (Abbott Laboratories Diagnostic Division). For purposes of this study, we extracted data describing serum concentrations of creatine kinase (CK), aspartate aminotransferase (AST), and myoglobin because these constituents are normally concentrated in muscle, but leak into blood circulation for some time after muscle damage; their level in blood provides a rough indication of the extent of muscle fiber destruction (Cardinet 1997; Hulland 1993). This well-established relationship is the basis for wide usage of these serum constituents as diagnostic markers of muscle injury in human and veterinary medicine (Kiessling et al. 1981; Krefetz and McMillin 2005; Latimer et al. 2003). We characterized muscle injury as significant if serum enzyme levels exceeded reference values (Teare 2002) for captive grizzly bears (18–142 U/liter for AST [$n = 139$] and 0–387 U/liter for CK [$n = 50$]).

We fitted bears with either a Televilt Simplex Global Positioning System (GPS) radiocollar (Televilt; TVP Positioning AB, Lindesberg, Sweden) or an Advanced Telemetry Systems GPS radiocollar (Advanced Telemetry Systems, Inc., Isanti, Minnesota). We programmed the majority of radiocollars to acquire 3-dimensional locations at 4-h time intervals; however, some collars were programmed for shorter intervals ranging from 1 to 3 h. Our research protocol was reviewed and approved by the University of Saskatchewan's Committee on Animal Care and Supply, and was in accordance with guidelines provided by the American Society of Mammalogists' Animal Care and Use Committee (Gannon et al. 2007) and the Canadian Council on Animal Care (2003) for the safe handling of wildlife.

Pisgah Bear Sanctuary Black Bear Research Project.—We captured 213 American black bears 363 times between May 1981 and August 2002 (research goals are summarized by Powell et al. [1997]) in the 220-km^2 Pisgah Bear Sanctuary, located on the Pisgah National Forest approximately 35 km southwest of Asheville, North Carolina (35°28′N, 82°40′W) in the southern Blue Ridge Mountains of the Southern Appalachians. Captured bears were composed of 80 females (1–11 years old at 1st capture) with 50 juvenile bears (<3 years old) and 30 adults (≥3 years old) and 133 males (1–15 years old at 1st capture) with 98 juveniles and 35 adults.

We used Aldrich-type leghold snares for 351 captures and barrel traps for 12 captures (Powell 2005). The leghold snares were modified with automobile hood springs to provide cushioning for trapped bears (Johnson and Pelton 1980). Bears were anesthetized by pole syringe or blowpipe using a 2:1 mixture of ketamine hydrochoride (Fort Dodge Animal Health, Overland Park, Kansas) and xylazine hydrochloride (Phoenix Pharmaceutical Inc., St. Joseph, Missouri), with approximately 200 mg ketamine and 100 mg xylazine per milliliter, administered intramuscularly at a combined dosage of 12 mg/kg estimated body weight. We monitored vital signs (body temperature, pulse rate, and respiration rate) continuously during the first 20–30 min of handling and every 5–10 min thereafter. We gave all bears ear tags and tattoos and recorded standard measurements. We weighed bears slung beneath a load scale and measured body length as distance from tip of nose to end of last tail vertebra following the curvature of the back. We extracted a premolar tooth to estimate age by counting cementum annuli (Stoneberg and Jonkel 1966) and drew blood from the femoral vein into sterile tubes for biochemical analysis and into an ethylenediaminetetraacetic acid tube for determination of the complete blood count. Blood samples were placed on ice immediately after collection and delivered to Mission Memorial Hospital in Asheville, North Carolina, within 1.5 h for laboratory analyses using standard hospital protocols. For this study, we extracted data describing serum concentrations of CK and AST. Serum myoglobin was not measured in blood samples collected from black bears. We characterized muscle injury as significant if serum enzyme levels exceeded reference values (Teare 2002) for captive black bears (0–205 U/liter for AST [$n = 135$] and 0–421 U/liter for CK [$n = 90$]).

We fitted 154 bears with very-high-frequency (VHF) radiocollars (made by multiple manufacturers over the course of >20 years), according to research goals at the time of capture. By driving the Blue Ridge Parkway, which bisected the study area, we could estimate locations of up to 12 bears in 2 h. We estimated locations of bears as the arithmetic mean of azimuths recorded within 15 min, unless a bear was inactive, in which case we sometimes extended the time limit. We located bears in blocks of four, six, or twelve 2-h periods, depending on objectives for our research in a given year, while attempting to reduce temporal autocorrelation among blocks (location estimates exhibited independence after 28–33 h—Swihart and Slade 1985). Using this schedule, we could obtain nearly 400 location estimates for bears followed during an entire active season. The bears' collars indicated activity or inactivity. Angle error was leptokurtotic around 0° and median error for location estimates was approximately 250 m (Zimmerman and Powell 1995). Our protocol for handling bears was approved by the Institutional Animal Care and Use Committees of North Carolina State University and Auburn University; was in accordance with the principles and guidelines of the of the American Society of Mammalogists' Animal Care and Use Committee (Gannon et al. 2007), with the Animal Behavior Society (2003), and with the Canadian Council on Animal Care (2003); and met the criteria for animal welfare of livetrapped mammals set by Powell and Proulx (Powell 2005; Powell and Proulx 2003).

Statistical analyses.—We performed statistical analyses under 3 broad themes: capture and muscle injury; effect of capture on mobility; and effect of repeated captures on body condition. Sample sizes varied between analyses depending on completeness of records or constraints imposed on the analysis. Details for specific analyses including sample sizes are as follows.

Muscle injury and survival.—We used program MARK (White and Burnham 1999) to estimate sex-specific survival rates in grizzly bears and American black bears and to determine if high AST concentration at capture was associated with lower individual survival. We selected AST as a covariate instead of myoglobin because it was measured in both species.

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Although CK also was measured in both species, determination of serum kinetics in humans (Krefetz and McMillin 2005) and domestic mammals (Latimer et al. 2003) show that AST remains elevated in blood for a longer duration than CK after muscle injury, that is, 5–7 days versus 1–2 days. Thus, we assumed AST levels in bears would better reflect severity of injury, especially in bears captured by leghold snare or barrel trap where time lapsed between capture and blood collection could be prolonged, that is, as long as 16 h.

We created encounter histories based on 1-month intervals for 56 grizzly bears (30 females and 26 males) captured during 1999–2003 and on 1-year intervals for 103 black bears (42 females and 61 males) captured during 1981–2002. We used the Barker model, a generalization of the joint live and dead encounters model (Burnham 1993), that allows live resightings (either visually or by radiotelemetry) and deaths to be reported at any time during the open period between capture and recapture (Barker 1997). This model parameterizes capture–recapture and tag mortality jointly by estimating both survival (S), which is the probability that an animal survives between 2 sampling occasions, and the probability of recapture (p). In addition, this model estimates the probabilities that a tag will be reported given that the individual was found dead (r), a resighting will occur within the study period (R), an animal will be resighted and then die within the study period (R'), an animal will remain in the study area (F), and an animal will temporarily emigrate from the study area (F'). We used a logit link in the analyses of both species, and we excluded from the analyses any data collected during the winter (denning) months.

For the analysis of grizzly bears, we reduced the available sample to 56 bears that were captured in a central portion of the study area between 1999 and 2003 to ensure that all bears had a defined area of initial capture during the time period of the survival analysis. All of these bears had been fitted at capture with either a GPS radiocollar, a VHF ear radiotransmitter (Advanced Telemetry Systems, Inc.), or both devices. We captured bears in the central study area continuously throughout the study period, so all bears had the potential to be recaptured by helicopter darting or by leghold snare, or to be ''resighted'' by GPS locations or by VHF signals received during telemetry flights. Recoveries of dead bears were based on investigation of potential mortalities during monthly flights for GPS collar uploads and tracking of VHF ear radiotransmitters as well as any incidental finding of dead bears. Bears of unknown fate included bears that removed their radiotransmitter devices or emigrated from the central study area, as well as bears with radiotransmitter devices that malfunctioned or were destroyed, for example, by poachers. Monthly sampling intervals were used because this time interval corresponded best with the occurrence of radiotelemetry flights and captures.

To develop models, we 1st reduced the number of parameters by fixing the movement parameters, F and F', to create simpler movement models including permanent emigration ($F' = 0$) and random emigration ($F' = F = 1$), as well as a more complex Markov emigration model (Barker and White 2001). We added to these base models by including sex and mean age of bear during the study as covariates. This was justified because other studies of bears have shown that these biological factors can influence survival rates and capture probabilities (Hovey and McLellan 1996). Although we held the parameters in most models constant over time, we also included a model that allowed recapture rate to be higher during spring than during fall, which was consistent with our capture efforts. We then used the model most supported by the data to test the effect of AST on bear survival.

For the analysis of black bears, we used a sample of 103 radiocollared bears for which serum AST results were available. Resightings for the Barker model were composed of VHF signals received during summers 1981–2002. The recovery of dead bears was based on mortality information from the North Carolina Wildlife Resources Commission and from field observations. Annual sampling intervals were used because this time interval corresponded best with telemetry and trapping schedules.

Similar to the analyses of grizzly bears, we initially determined the most-supported Barker movement model. We used a base model in which survival varied by sex and capture probability varied by age. Because juvenile black bears were less likely to be collared than were adult bears, we varied the resighting parameters by age. After the best-supported movement model was determined, we expanded our analyses by including AST as an individual covariate to survival. We did not consider time variation in any parameters given the restriction of model complexity based upon our relatively small sample size of marked bears. For both species, we used sample-size–adjusted Akaike Information Criterion (AIC_C) model selection (Burnham and Anderson 1998) to determine which models were most supported by the data, that is, ΔAIC_C values ≤ 2. We evaluated AIC_C weights for each model, which provided strength of evidence for model selection. We did not test goodness-of-fit because no reliable means of testing model fit currently exist for models developed using Barker's parameterization (R. Barker, pers. comm.).

Mobility after capture.—For this analysis, we tested the hypothesis that capture and handling of bears causes a measurable decrease in daily movement rates in the days after capture. We calculated movement rates (m/h) for grizzly bears as straight-line distance (m) between consecutive locations, recorded every 1–4 h with dilution of precision values ≤ 5, divided by time interval (h). We calculated movement rates (m/h) for American black bears as straight-line distance between consecutive locations, recorded $\leq$33 h apart, divided by time interval. For both species, we calculated daily movement rates as the average of all movement rates ($\leq$12 rates per day) recorded on a given day for an individual bear. We justified averaging of movement rates within a day because large variation in movement rates caused by daily activity patterns (e.g., diurnal and nocturnal activity patterns) was irrelevant to this analysis. For grizzly bears, we limited captures to those occurring between 1 April and 31 July because this was when $\geq$85% of captures occurred. We also limited calculation of movement rates to $\leq$100 days after capture for individual bears

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so, in effect, analyses of movement rates covered the period from April to October. For black bears, we further limited movement rates to bears tracked for $\geq$10 days after capture. Finally, we log-transformed movement rates to help meet the assumption of equal variances of response values across the range of predictor variables.

We used a random coefficient mixed-model analysis of covariance to test for decreased movement rates among grizzly bears and black bears recently captured and radiocollared (Milliken and Johnson 2002). We fitted polynomial (quadratic and cubic) curves to daily movement rates as a function of days after capture ($\leq$100) for each bear on the assumption that, if capture affected movement rates for an individual bear, its daily movement rate would increase for a time after capture before reaching a plateau. We also investigated the fit provided by linear terms, which would suggest that movement rates increase indefinitely after capture. Conceptually, the sample space for the analysis was the ''population'' of bear response curves after capture. We nested response curves of individual bears to allow variance estimation with bears as the sample unit and to avoid pseudoreplication and repeated-measure issues with pooling locations from individual bears (Littell et al. 1996; Verbeke and Molenberghs 2000). In constructing models for each species, we considered effects of other factors and covariates, as well as interactions between factors, on daily movement rate (Stenhouse et al. 2005) including day and month of capture, sex and reproductive class (male, female, or female with dependent offspring), method of capture, the number of times a bear was captured in a given year, and duration between location fixes. We modeled seasonal changes in movement rate by estimating month-specific and month $\times$ day of month interaction terms to account for potential differences in movement rate patterns of bears with home ranges at different elevations, for example, alpine versus agricultural areas.

We used AIC_C model selection (Burnham and Anderson 1998) and considered models with ΔAIC_C values $\leq$ 2 most supported by the data. The effective sample size of AIC_C calculations was the number of unique bears in the analysis. We primarily used AIC_C methods to select appropriate models rather than hypothesis tests of individual parameters to avoid statistical issues when combining 2 methods of model selection (Lukacs et al. 2007). Strength of relationships was evaluated by plotting topical covariates and associated confidence intervals (Burnham and Anderson 1998).

After finding the most-supported model, we added AST (for both species) and myoglobin (for grizzly bears) levels to the model to see if these indicators of muscle injury were significant covariates. Because AST and myoglobin values were not available for all captures of bears, sample sizes for these analyses were smaller than for the movement rate analyses. Therefore, we recalculated AIC_C parameters for the most-supported models ($\Delta AIC_C \leq 2$) using reduced data sets to compare with models that included AST or myoglobin as covariates.

Body condition and repeated captures.—For this analysis, we tested the hypothesis that age-related changes in the body condition of bears are affected negatively by the number of times a bear is captured. In other words, if the general trend is for body condition to increase with age when controlling for other potentially confounding factors (e.g., year of capture), the rate of increase will be less for bears captured repeatedly than for bears captured 1 time only. To quantify body condition, we calculated a body condition index (BCI) for grizzly bears and American black bears using a model of the form:

$$\mathrm{BCI} = \frac{\mathrm{M} - 3.21\mathrm{L} + 11.64}{0.29 + 0.017\mathrm{L}},$$

where M is the natural log of body mass (kg) and L is the natural log of body length (cm—Cattet et al. 2002). This model predicts the standardized residual from the regression of body mass against body length, an index of body condition strongly correlated with true body condition in black bears ($R^2 = 0.93$, $P < 0.001$, $n = 33$), defined as the combined mass of fat and skeletal muscle relative to body size.

We used a mixed-model repeated-measures analysis of covariance to determine if changes in BCI values differed as a function of number of times a bear was captured (Milliken and Johnson 2002). We assumed that body condition of a bear also might change with age, reproductive status, and environmental conditions. So, in constructing models for each species, we considered effects of other factors and covariates on BCI values including age, sex and reproductive class, year of capture, as well as the interaction between number of times captured and year of capture. The interaction term allowed changes in BCI to differ as a function of the number of times a bear was captured. We tested models with year of capture as both a linear term (YR) and a quadratic term (YR^2) to determine if number of times captured affected slope of the age–body condition relationship (i.e., a linear effect), or shape of the curve (i.e., a quadratic effect), or both. For bears inadvertently captured more than once within a single year, we considered BCI values recorded at 1st capture of the year only. In addition, because the interval between subsequent captures for bears captured more than once was variable, we only considered models with covariance structures that allow unequal intervals between observations, for example, spatial, unstructured, and compound symmetry models (Milliken and Johnson 2002). We used AIC_C model selection and considered only models with ΔAIC_C values $\leq$ 2 to be most supported by the data. The effective sample size was the number of unique bears in the analysis.

An implicit assumption in this analysis was that bears captured repeatedly were a random sample of the population such that the probability of being captured was not affected by their body condition. However, should bears in poor condition be more likely to be lured to snare sites or barrel traps by the presence of bait and consequently captured than bears in good condition, this assumption would be incorrect and our hypothesis would fall. To test this assumption, we removed helicopter capture records from the grizzly bear data set, and used the Burnham (1993) joint live-and-dead encounter model in program MARK (White and Burnham 1999) to explore effects of body condition on grizzly bear and black bear recap-

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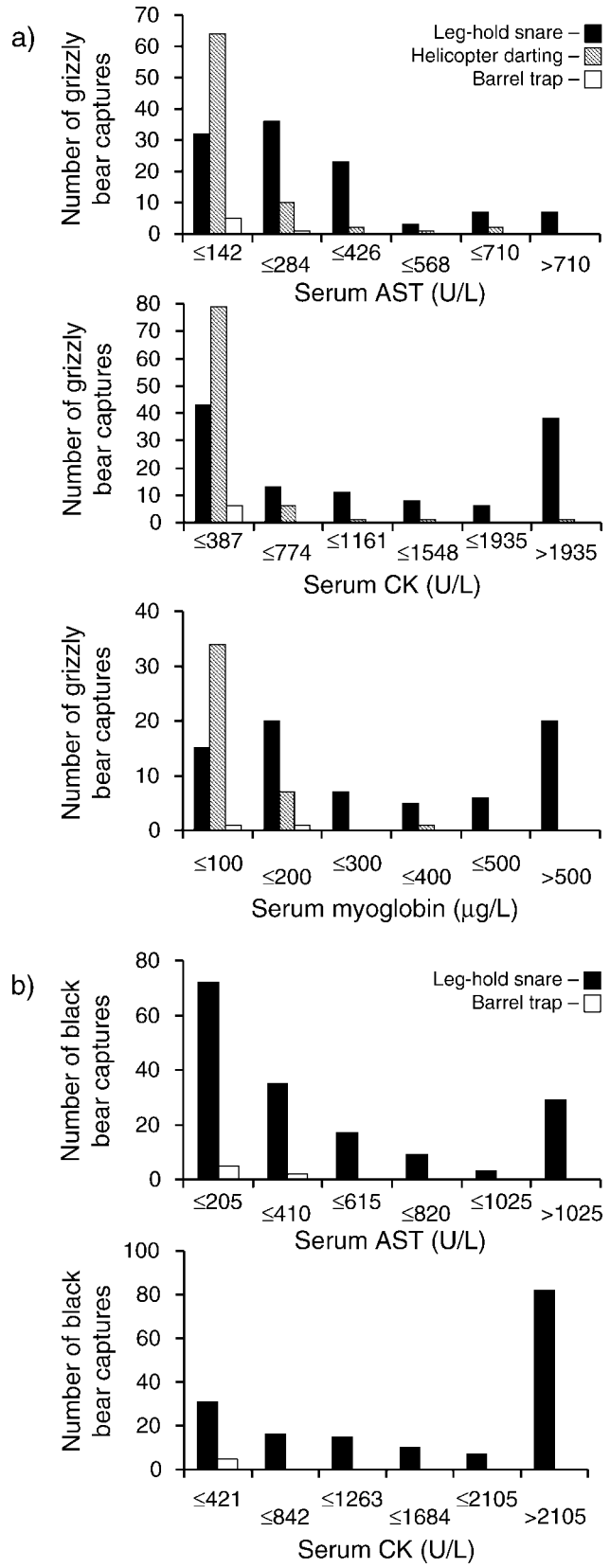


Fig. 1.—a) Serum concentrations of aspartate aminotransferase (AST), creatine kinase (CK), and myoglobin recorded at 213 grizzly bear captures for the Foothills Model Forest Grizzly Bear Project in western Alberta, Canada (1999–2005). Values were recorded for bears captured by leghold snare ($n = 119$), helicopter darting ($n = 87$), and barrel trap ($n = 7$). Cut points for intervals represent multiples of the upper limit of the reference interval for captive grizzly bears for AST (142 U/liter) and CK (387 U/liter—Teare 2002). A reference interval for serum myoglobin has not been established for grizzly bears. b). Serum concentrations of AST and CK recorded at 172 black bears captures for the Pisgah Bear Sanctuary Black Bear Research Project in North Carolina (1981–2002). Values were recorded for bears captured by leghold snare ($n = 165$) and barrel trap ($n = 7$). Cut points for intervals represent multiples of the upper limit of the reference interval for captive black bears for AST (205 U/liter) and CK (421 U/liter—Teare 2002). Serum myoglobin was not measured for black bears.

ture rates. The Burnham model estimates the same parameters as the Barker model with exception of sighting probabilities (R and R'). Radiotelemetry sightings were not used with the Burnham model and therefore sighting probabilities are not relevant. In addition, the Burnham model estimates a single fidelity parameter (F). The most-supported biological model for each species from the Barker analysis described above in the "*Muscle injury and survival*" section was used as a base model for this analysis. The mean BCI value of bears was entered as a covariate to recapture rate and slope (β) estimates of the BCI-covariate term were then used to evaluate for a potential relationship between recapture rate and BCI.

Results

Capture-related muscle injury.—We had serum chemistry results available from 213 grizzly bear and 172 American black bear captures. Serum concentrations of aspartate AST, CK, and myoglobin were greater in grizzly bears captured by leghold snare than in bears captured by helicopter darting (Fig. 1a; mean, median, and range, respectively: AST—288 U/liter, 198 U/liter, and 41–1,665 U/liter versus 128 U/liter, 96 U/liter, and 34–702 U/liter; CK—3,197 U/liter, 807 U/liter, and 31–37,280 U/liter versus 213 U/liter, 117 U/liter, and 31–3,838 U/liter; myoglobin—497 μg/liter, 231 μg/liter, and 24–7,184 μg/liter versus 65 μg/liter, 40 μg/liter, and 15–341 μg/liter) or by barrel trap (AST—115 U/liter, 113 U/liter, and 69–166 U/liter; CK—283 U/liter, 104 U/liter, and 43–1,399 U/liter). Values for AST exceeded the upper limit of the reference interval for captive grizzly bears (142 U/liter) in 70% of samples collected from 119 leghold-snare captures, 18% of samples from 87 helicopter-darting captures, and 14% of samples from 7 barrel-trap captures. Values for CK exceeded the upper limit of the reference interval for captive grizzly bears (387 U/liter) in 64% of samples collected from leghold-snare captures, 14% of samples from helicopter-darting captures, and 14% of samples from barrel-trap captures. A reference interval for serum myoglobin has not been established for grizzly bears.

Serum concentrations of AST and CK were greater in American black bears captured by leghold snare than in bears captured by barrel trap (Fig. 1b; AST—575 U/liter, 247 U/liter, and 39–5,340 U/liter versus 132 U/liter, 91 U/liter, and 44–331 U/liter; CK—10,297 U/liter, 2,242 U/liter, and 39–109,780 U/liter versus 1,708 U/liter, 235 U/liter, and 89–6,540 U/liter).

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TABLE 1.—Models selected using sample-size–adjusted Akaike Information Criterion (AIC_C) to test the hypothesis that the serum aspartate aminotransferase (AST) concentration of a) grizzly bears captured for the Foothills Model Forest Grizzly Bear Research Project in western Alberta, Canada (1999–2005), and b) American black bears captured for the Pisgah Bear Sanctuary Black Bear Research Project in North Carolina (1981–2002) at the time of capture affected survival. The analyses are based on the capture records and resight data (by visual or radiolocation) for 57 grizzly bears and 103 black bears.

No.	Model[a,b]	AIC_C	ΔAIC_C	w_i[c]	K[d]
a) Grizzly bears					
1	S(SEX + AST) p(SEX) r(AGE) R(.) R'(.) $F = F' = 1$	2,072.6	0.00	0.46	9
2	S(SEX × AST) p(SEX) r(AGE) R(.) R'(.) $F = F' = 1$	2,073.8	1.21	0.25	10
3	S(SEX) p(SEX) r(AGE) R(.) R'(.) $F = F' = 1$	2,074.0	1.35	0.24	8
4	S(SEX + AGE) p(SEX + AGE) r(AGE) R(.) R'(.) $F = F' = 1$	2,078.0	5.34	0.03	10
5	S(SEX) p(SEX) r(.) R(.) R'(.) $F = F' = 1$	2,079.1	6.50	0.02	7
6	S(SEX × AGE) p(SEX × AGE) r(AGE) R(.) R'(.) $F = F' = 1$	2,080.6	7.97	0.01	12
7	S(AGE) p(AGE) r(AGE) R(.) R'(.) $F = F' = 1$	2,080.6	8.00	0.01	8
8	S(SEX) p(SEX) r(.) R(.) R'(.) F(.) F'(0)	2,081.2	8.55	0.01	8
9	S(.) p(.) r(.) R(.) R' (.) $F = F' = 1$	2,082.1	9.44	0.00	5
10	S(SEX) p(SEX) r(.) R(.) R'(.) F(.) F' (.)	2,083.2	10.62	0.00	9
11	S(SEX) p(SEX) r(AGE) R(.) = R'(.) $F = F' = 1$	2,084.3	11.69	0.00	6
b) American black bears					
1	S(SEX) p(AGE) r(.) R(AGE) R'(AGE) F(.) F'(.)	1,200.6	0.00	0.25	11
2	S(SEX × AST) p(AGE) r(AGE) R(AGE) R'(AGE) F(.) F'(.)	1,201.0	0.46	0.20	14
3	S(SEX + AST) p(AGE) r(AGE) R(AGE) R'(AGE) F(.) F'(.)	1,201.7	1.17	0.14	13
4	S(SEX × AST) p(AGE) r(.) R(AGE) R'(AGE) F(.) F'(.)	1,201.8	1.20	0.14	13
5	S(AST) p(AGE) r(AGE) R(AGE) R'(AGE) F(.) F'(.)	1,202.6	2.07	0.09	12
6	S(SEX) p(SEX) r(.) R(SEX) R'(SEX) F(.) F'(.)	1,203.3	2.71	0.06	11
7	S(SEX) p(SEX) r(.) R(AGE) R'(AGE) F(.) F'(.)	1,203.9	3.36	0.05	11
8	S(SEX × AST) p(SEX + AGE) r(.) R(AGE) R'(AGE) F(.) F'(.)	1,204.4	3.78	0.04	15
9	S(SEX) p(AGE) r(.) R(AGE) R'(AGE) $F = F' = 1$	1,205.6	4.98	0.02	11
10	S(SEX) p(AGE) r(.) R(AGE) R'(AGE) F(.) F'(0)	1,207.7	7.17	0.01	11
11	S(.) p(.) r(.) R(.) R'(.) F(.) F'(.)	1,210.3	9.76	0.00	7

[a] Model parameters are S = survival, p = capture probability, r = the recovery or reporting rate of dead bears, and R and R' = the probability of resighting a bear, either visually or by radiolocation. The movement parameters F and F' indicate permanent emigration when $F' = 0$, random emigration when $F' = F = 1$, and Markov emigration when F(.) F'(.).

[b] Variables are SEX = sex and AGE = mean age of bear during study; (.) is a parameter-specific constant; + and × denote additive and interactive effects, respectively.

[c] AIC weight.

[d] Number of estimable parameters in model.

Values for AST exceeded the upper limit of the reference interval for captive black bears (205 U/liter) in 66% of samples collected from 165 leghold-snare captures and 29% of samples from 7 barrel-trap captures. Values for CK exceeded the upper limit of the reference interval for captive black bears (421 U/liter) in 81% of samples collected from leghold-snare captures and 29% of samples from barrel-trap captures. Serum myoglobin was not measured in samples collected from black bears.

Serum enzymes and myoglobin were positively correlated in grizzly bears (Pearson correlation: AST versus CK—$R = 0.80$, $P \leq 0.001$, $n = 193$; AST versus myoglobin—$R = 0.69$, $P \leq 0.001$, $n = 116$; CK versus myoglobin—$R = 0.57$, $P \leq 0.001$, $n = 117$). Similarly, AST and CK were positively correlated in black bears ($R = 0.82$, $P \leq 0.001$, $n = 172$). For captures by leghold snare, serum concentrations of CK or AST did not correlate with body mass for grizzly bears (Pearson correlation: $P \geq 0.13$, $n = 73$) or black bears (Pearson correlation: $P \geq 0.62$, $n = 163$).

Muscle injury and survival.—Of 56 grizzly bears used in the analysis, 29 were captured by remote drug delivery (28 from a helicopter and 1 from the ground), 25 by leghold snare, and 2 by barrel trap. The sample was composed of 30 females (mean ± *SD*, range, respectively; age = 8.1 ± 5.9 years, 1.9–21.7 years) and 26 males (5.9 ± 4.2 years, 1.0–17.1 years). Mean AST concentration was 249 U/liter (*SD* = 253.6 U/liter, range = 38–1,248 U/liter) with 55% of values > 142 U/liter, the upper limit of the reference interval for captive grizzly bears (Teare 2002).

We developed age-specific survival models in a progressive manner that began with 1st determining which model described movement pattern of grizzly bears best, that is, permanent, random, or Markov emigration (Table 1a). Support was stronger for a random emigration model ($F = F' = 1$, model 5) than for permanent emigration ($F' = 0$, model 8) or Markov emigration models (model 10). We determined next if a random emigration model was affected by the biological covariates sex and mean age of bear during the study. Support was stronger for model 3, a model in which survival and capture probability varied by sex and reporting rate varied by age, than for model 9, a model that does not include biological covariates. The final step was to determine if a biologically appropriate random emigration model was affected by the muscle-injury covariate AST. For bears captured more than once, this was the AST value recorded at last capture. Overall, support was strongest for model 1, in which AST had an additive effect on survival. A

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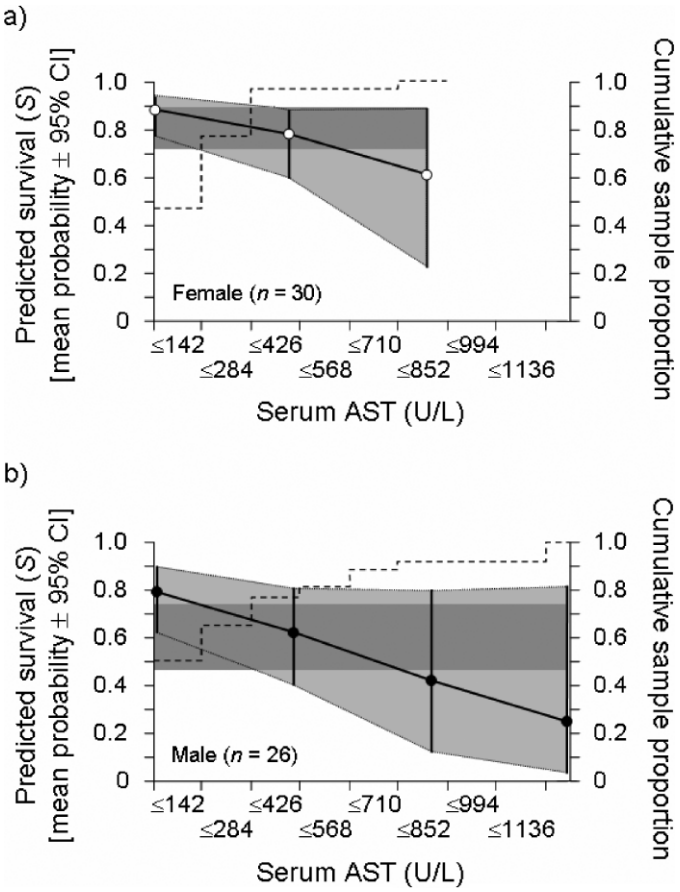


FIG. 2.—Probability of survival for grizzly bears as a function of their serum concentration of aspartate aminotransferase (AST) at capture predicted by model 1 of Table 1a. Predicted survival rates were estimated from the records of a) 30 female and b) 26 male grizzly bears captured for the Foothills Model Forest Grizzly Bear Project in western Alberta, Canada, during 1999–2003. Cut points for intervals represent multiples of the upper limit (142 U/liter) of the reference interval for AST in captive grizzly bears (Teare 2002) with the highest value (1,248 U/liter) at >8 times the reference interval. Light-shaded areas represent sex-specific 95% confidence intervals for model 1 of Table 1a and dark-shaded areas represent sex-specific 95% confidence intervals for model 3, a model for which AST had no significant effect on survival but also was supported by the data ($\Delta AIC_C = 1.35$, $w_i = 0.24$). The dashed lines denote the cumulative proportions of sampled female and male bears falling within the increasing range of AST intervals. We interpret these results to indicate that high AST levels may affect survival of some grizzly bears, but if it does, reduced survival is more likely affected by altered mobility and behavior than by direct physiological effects, for example, circulatory collapse. The large confidence intervals around survival estimates at higher AST levels reflect both the small sample sizes at these levels and the variation in responses among individual bears.

model in which AST and sex had an interactive effect on survival (model 2) also was supported by the analysis. However, it did not differ in strength of support from model 3, which did not include any (AST) survival effects.

Using model 1, we plotted predicted survival curves with associated 95% confidence intervals (95% *CI*s) for female and male grizzly bears with AST values ranging from 0 to 1,200 U/liter, which approximates the observed range of 38–1,248 U/liter (Fig. 2). Although mean survival rate decreased as AST values increased in both female and male grizzly bears, the overall effect was weak given overlap in confidence intervals between different AST values and broadening of confidence intervals as AST values increased. The larger confidence intervals at higher AST values reflected to some extent the small proportion of bears (9% or 5 of 56 bears) with AST values $\geq$ 6 times the reference interval for captive grizzly bears. At the end of the study, 13 of 31 bears with AST levels $>$ 142 U/liter were alive, 7 bears died, and the fate of 11 other bears was unknown. Of the 7 deaths, 3 were legal by hunting or in defense of life or property, 2 were illegal, and 2 were of unknown cause with carcasses recovered at 1 week and 3 weeks after capture.

Of 103 black bears used in the analysis, 102 were captured by leghold snare and 1 was captured by barrel trap. The sample was composed of 42 females (mean $\pm$ *SD*, range, respectively; age = 5.4 $\pm$ 3.1 years, 1.0–14.0 years) and 61 males (3.8 $\pm$ 2.4 years, 1.0–11.4 years). The mean AST concentration was 594 U/liter (*SD* = 911.0 U/liter, range = 39–5,340 U/liter) with 59% of values $>$ 205 U/liter, the upper limit of the reference interval for captive black bears (Teare 2002).

Following the same procedure used in the grizzly bear survival analysis, we found stronger support for a Markov emigration model (model 1; Table 1b) than for permanent (model 10) or random emigration models (model 9). When considering potential effects of biological covariates, support was stronger for models where survival varied by sex, and capture and resighting probabilities and recovery rate varied by age than for a model without biological covariates (model 11). We did not find, however, substantial support for AST as a covariate (model 1).

Mobility after capture.—We used capture and movement records of 91 grizzly bears captured 150 times for AIC_C model selection. Multiple models were supported, with many including capture-effect terms (Table 2a). The highest-ranked models ($\Delta AIC_C \leq 2$) indicated that movement rates varied as a function of sex and reproductive class (female, female with dependent offspring, or male), month, the interaction between month and day of month, and the number of days after capture. The month $\times$ day of month interaction suggested that trends in movement rates within months may have differed between bears, particularly during April and May, possibly as a result of occupying home ranges across a wide elevational gradient, that is, $>$ 1,600 m. An interaction term between method of capture and number of days after capture was supported by model 2, but the biological significance of this term was questionable because model 1 was better supported with fewer capture variables. A model without capture variables (model 10) was not supported by the data.

Predicted movement rate for grizzly bears as a function of the number of days after capture was represented best by a polynomial curve (Fig. 3a). Because movement rates always stabilized before 70 days after capture, we assumed that the movement rate at 70 days was equivalent to the mean population movement rate for a given sex and reproductive

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TABLE 2.—Models selected using sample-size–adjusted Akaike information criterion (AIC_C) to test the hypothesis that the capture and handling of a) grizzly bears for the Foothills Model Forest Grizzly Bear Research Project in western Alberta, Canada (1999–2005), and b) American black bears for the Pisgah Bear Sanctuary Black Bear Research Project in North Carolina (1981–2002) caused a measurable decrease in their daily movement rates in the days after capture. The analyses are based on capture and movement records for 91 grizzly bears captured 150 times and 128 black bears captured 196 times.

No.	Variables[a]		AIC_C	ΔAIC_C	w_i[b]	K[c]
	Biological and sampling	Capture				
a) Grizzly bears						
1	REP, MON_C, $MON_C \times DAY_M$	DAY_C, DAY_C^2, DAY_C^3	22,897.7	0.0	0.64	17
2	REP, MON_C, $MON_C \times DAY_M$	DAY_C, DAY_C^2, DAY_C^3, CAP × DAY_C	22,899.5	1.8	0.26	18
3	REP, MON_C, $MON_C \times DAY_M$	DAY_C, DAY_C^2, DAY_C^3, REP × DAY_C	22,901.6	3.9	0.09	19
4	MON_C, $MON_C \times DAY_M$	DAY_C, DAY_C^2, DAY_C^3, REP × DAY_C	22,909.9	12.2	0.00	17
5	REP, MON_C	DAY_C, DAY_C^2, DAY_C^3	22,923.3	25.6	0.00	13
6	REP, MON, MON^2	DAY_C, DAY_C^2, DAY_C^3	22,931.3	33.6	0.00	12
7	REP, MON_C, $MON_C \times DAY_M$	DAY_C, DAY_C^2	22,934.6	36.9	0.00	16
8	REP, DAY_J	DAY_C, DAY_C^2, DAY_C^3	22,943.6	46.0	0.00	11
9	REP, MON, MON × DAY_M	DAY_C, DAY_C^2, DAY_C^3	22,945.7	48.0	0.00	15
10	REP, MON_C, $MON_C \times DAY_M$		22,958.9	61.2	0.00	14
b) American black bears						
1	FIX, REP, MON, AGE	DAY_C, DAY_C^2, DAY_C^3	9,937.6	0.0	0.28	13
2	FIX, REP, MON	DAY_C, DAY_C^2, DAY_C^3, DAY_C × MON	9,938.2	0.6	0.21	13
3	FIX, REP, MON	DAY_C, DAY_C^2, DAY_C^3	9,939.0	1.4	0.14	12
4	FIX, REP, MON^2	DAY_C, DAY_C^2, DAY_C^3	9,939.4	1.8	0.11	12
5	FIX, REP, MON	DAY_C, DAY_C^2, DAY_C^3, DAY_C × AGE	9,940.3	2.7	0.07	13
6	FIX, REP, MON	DAY_C, DAY_C^2, DAY_C^3	9,940.9	3.3	0.05	14
7	FIX, REP, MON	DAY_C, DAY_C^2, DAY_C^3, DAY_C × CAP	9,941.5	3.9	0.04	13
8	FIX, REP	DAY_C, DAY_C^2, DAY_C^3	9,941.7	4.1	0.04	11
9	FIX, REP, MON_C	DAY_C, DAY_C^2, DAY_C^3	9,941.8	4.2	0.03	16
10	FIX, REP, MON, AGE		9,960.0	22.4	0.00	10

[a] Variables are AGE = age in years, CAP = capture method (leghold snare and helicopter darting for grizzly bears, and leghold snare and barrel trap for black bears), DAY_C = number of days after capture, DAY_J = Julian day, DAY_M = day of month, FIX = time interval between location fixes in hours, MON = month as a continuous variable, MON_C = month as a categorical variable, REP = sex and reproductive class (male, female, or female with dependent offspring), and × indicates an interaction term.

[b] AIC weight.

[c] Number of estimable parameters in model.

class in a given month. Mean movement rate immediately after capture was approximately 57% of normal (95% *CI* = 45–74%) with slight differences between reproductive classes and months. Using a jackknife procedure to estimate standard errors on model 1, we determined movement rates to peak at 28 days (*SE* = 4.3 days, 95% *CI* = 20–37 days) after capture irrespective of sex and reproductive class or month of capture.

We used capture and movement records of 128 American black bears captured 196 times for AIC_C model selection. Multiple models were supported, with most including capture-effect terms (Table 2b). The highest-ranked models ($\Delta AIC_C \leq 2$) indicated that movement rates varied as a function of the time interval between location fixes, sex and reproductive class, month, age, and the number of days after capture. A model without capture variables (model 10) was not supported by the data.

As with grizzly bears, predicted movement rates for black bears as a function of number of days after capture was represented best by a polynomial curve in which movement rates increased after capture then settled to an approximate mean value (Fig. 3b). Mean movement rate immediately after capture was approximately 77% of normal (95% *CI* = 64–88%) with slight differences between reproductive classes and months. Using a jackknife procedure to estimate standard errors on the most-supported model, we determined movement rates to plateau at 36 days (*SE* = 8.6 days, 95% *CI* = 19–53 days) after capture irrespective of sex and reproductive class, month of capture, or age. We also found that the time interval between location fixes affected estimation of movement rates such that movement rates became less as the interval between location fixes increased.

Mobility and muscle injury.—We examined the potential effect of muscle injury on movement rates by including serum concentration of AST in both species, and myoglobin in grizzly bears, as an interaction term with number of days after capture in the most-supported models from Table 2. The data set for these analyses was reduced to 96 captures involving 50 unique bears because AST and myoglobin values were not available for all captures. A model with AST as a covariate was more supported than model 1 in Table 2a by 2.5 AIC_C units. However, a model with myoglobin as a covariate was not supported. As with the data for grizzly bears, the data set for black bears was reduced to 183 captures involving 63 unique bears. A model with AST as a covariate was more supported than model 1 in Table 2b by 3.9 AIC_C units. Inspection of plots suggested that initial movement rates were lower for all sex and reproductive classes in both species when AST concentrations were high, such that mean movement rates for bears with AST levels 3–4 times greater than the upper limit of the reference

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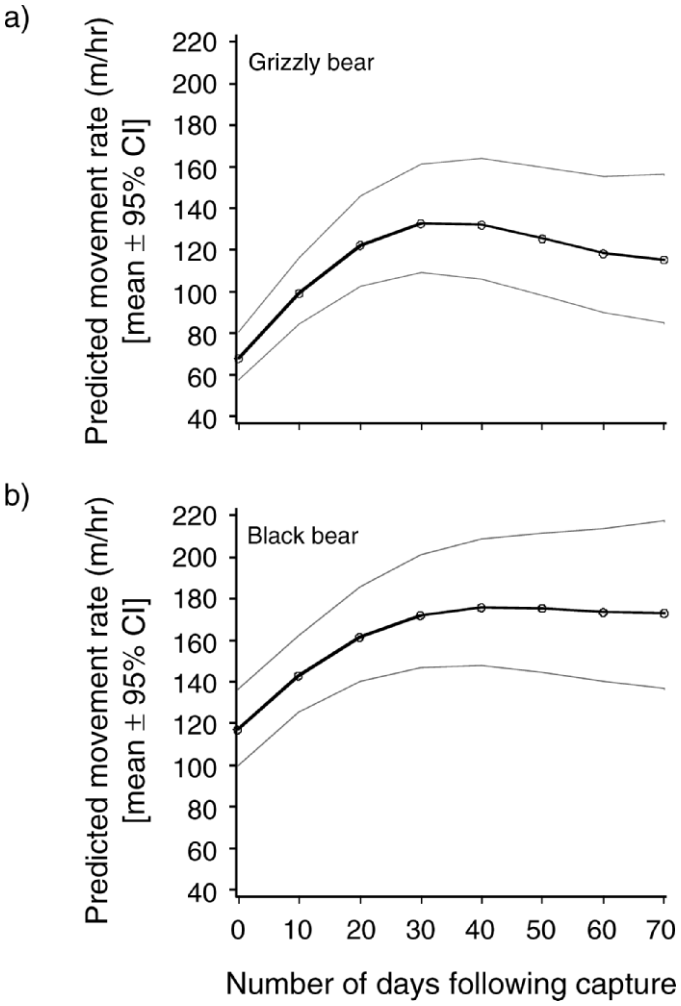


FIG. 3.—The movement rates for a) grizzly bears captured for the Foothills Model Forest Grizzly Bear Research Project in western Alberta, Canada (1999–2005), and b) American black bears captured for the Pisgah Bear Sanctuary Black Bear Research Project in North Carolina (1981–2002), as a function of the number of days after capture predicted from the most-supported model for each species in Table 2. The analyses are based on capture and movement records of 91 grizzly bears captured 150 times and 128 black bears captured 196 times. The plots are standardized for female grizzly bears (all ages) and female black bears (2.9 years old) without dependent offspring captured during the month of May.

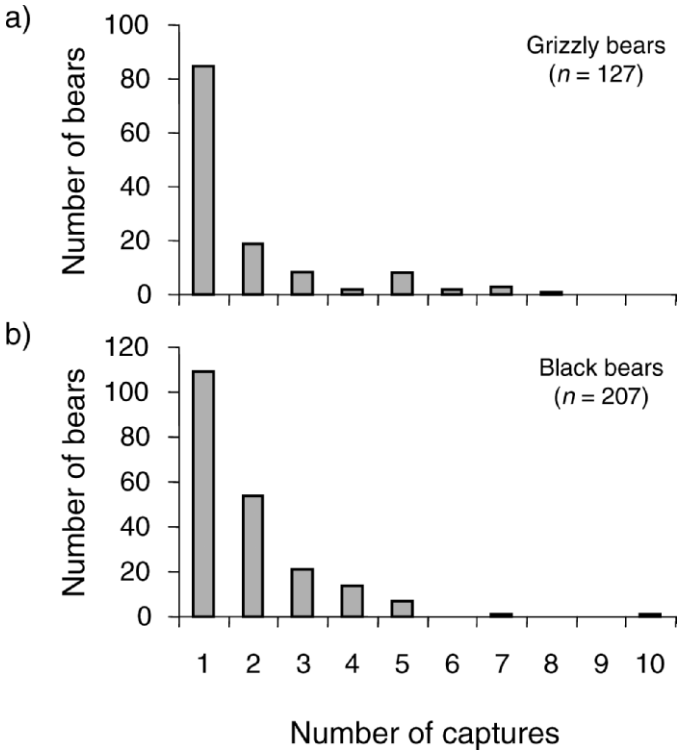


FIG. 4.—The numbers of individual a) grizzly bears and b) American black bears captured as a function of the number of captures occurring during the Foothills Model Forest Grizzly Bear Project in western Alberta, Canada (1999–2005), and the Pisgah Bear Sanctuary Black Bear Research Project in North Carolina (1981–2002).

interval were depressed approximately 20% more than mean movement rates for bears with normal AST levels.

Body condition and repeated captures.—We used capture records and BCI values from 127 grizzly bears captured 239 times to determine effect of repeated captures on body condition. Eighty-five bears were captured once only, whereas 42 bears were captured 2–8 times (Fig. 4a). Each sex and reproductive class (female, female with dependent offspring, or male) was adequately represented, that is, 28–50 bears per class. Multiple AIC_C models were supported, with the 4 most-supported models ($\Delta AIC_C \leq 2$) all including capture-effect terms (Table 3a). The highest-ranked model (model 1) indicated BCI values varied as a function of sex and reproductive class, age, year, number of times captured, and an interaction between number of times captured and year. Another model with no capture effects (model 5) was marginally supported ($\Delta AIC_C = 2.04$).

Mean BCI values generally increased with age in all reproductive classes (females, females with dependent offspring, or males). Rate of increase, however, was affected by the number of times a bear was captured such that bears captured repeatedly showed a slower rate of increase in BCI value with age than did bears captured once only (Fig. 5a). The difference in mean predicted BCI value between a 9-year-old bear captured once and a 9-year-old bear captured 5 times was 1.45, which is equivalent to a difference in body mass of approximately 25% (Cattet et al. 2002). The difference in body mass when captured 3 times was approximately 14%.

Ideally for Fig. 5, we should have shown predicted curves for all levels of multiple captures (2–10) encountered in this study. Doing so, however, would have resulted in either a single figure cluttered with many curves and overlapping confidence intervals, or a single figure with a cumulative curve (representing all capture levels ≥ 2) with a large error that would obscure any distinction with the curve for ''captured once only,'' or many additional figures with 1 for each capture level. We chose instead to show predicted curves for bears captured 5 times because this level was approximately midrange for number of captures per individual grizzly bear (2–8) and black bear (2–10). Because capture effect is directly

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TABLE 3.—The models selected using sample-size–adjusted Akaike information criterion (AIC_C) to test the hypothesis that changes over time in the body condition of a) grizzly bears captured for the Foothills Model Forest Grizzly Bear Research Project in western Alberta, Canada (1999–2005), and b) American black bears captured for the Pisgah Bear Sanctuary Black Bear Research Project in North Carolina (1981–2002) were affected by the number of times a bear was captured. The analyses are based on capture records and body condition index values for 130 grizzly bears captured 241 times and 207 black bears captured 299 times.

No.	Variables[a]		AIC_C	ΔAIC_C	w_i[b]	K[c]
	Biological and sampling	Capture				
a) Grizzly bears						
1	REP, AGE, YR, YR^2	NO, NO × YR^2	293.8	0.00	0.21	10
2	REP, AGE, YR, YR^2, MON	NO, NO × YR^2	294.3	0.50	0.17	11
3	REP, AGE, YR, YR^2	NO, NO × YR	294.5	0.70	0.15	10
4	REP, AGE, YR, YR^2	NO, NO × YR, CAP × YR	294.7	0.89	0.14	11
5	REP, AGE, YR, YR^2		295.9	2.04	0.08	8
6	REP, AGE, YR, YR^2, REP × AGE	NO, NO × YR^2	296.0	2.12	0.07	12
7	REP, AGE, YR, YR^2	NO × YR^2	296.5	2.70	0.06	9
8	REP, AGE^2, YR, YR^2	NO, NO × YR^2	296.7	2.90	0.05	10
9	REP, AGE, YR, YR^2	NO	297.2	3.35	0.04	9
10	REP, AGE, YR^2	NO × YR	297.7	3.85	0.03	9
b) American black bears						
1	REP, REP × YR, AGE, AGE × YR	NO, NO × YR	655.3	0.0	0.28	16
2	REP, REP × YR, AGE, AGE × YR	NO, NO × YR, CAP × YR	656.7	1.0	0.17	17
3	REP, REP × YR, AGE, AGE × YR	NO, NO × YR	657.2	1.4	0.14	12
4	REP, REP × YR, AGE, AGE × YR, MON	NO, NO × YR	657.6	1.9	0.11	17
5	REP, REP × YR, AGE, AGE × YR, REP × AGE	NO, NO × YR	657.9	2.2	0.09	20
6	REP, REP × YR, AGE, AGE × YR	NO_C, NO_C × YR	658.3	2.6	0.08	18
7	REP, REP × YR, AGE, AGE × YR		658.6	2.8	0.07	14
8	REP, AGE, AGE × YR	NO, NO × YR	659.7	3.9	0.04	12
9	REP, REP × YR, AGE, AGE × YR	NO × YR	660.9	5.1	0.02	15
10	REP, REP × YR, AGE, AGE × YR, REP × AGE		661.8	6.1	0.01	10

[a] Variables are AGE = age in years at time of capture, CAP = capture method, MON = month of capture, NO = number of times a bear was captured, NO_C = categorical number of times a bear was captured, REP = sex and reproductive class, YR = year of capture, and × indicates an interaction term.

[b] AIC weight.

[c] Number of estimable parameters in model.

proportional to number of times captured, however, one can interpolate that curves for capture levels from 2 to 4 fall between predicted curves shown in Fig. 5 and curves for capture levels > 5 fall below the curve for 5 captures.

To determine if a grizzly bear's body condition affected its probability of being captured, we used the most-supported biological covariate model (model 3 from Table 1a) with BCI added as a covariate for recapture rate to estimate a slope coefficient for the relationship between recapture rate and BCI, that is, S(SEX) p(SEX + BCI) r(AGE) F(.). The estimated logit-scale slope was 0.82 ($SE = 0.49$, 95% $CI = -0.14$–1.79), suggesting a positive relationship between recapture rate and BCI. Because a slope of 0 was within the confidence interval, however, we considered the relationship insignificant.

We used capture records and BCI values from 207 American black bears captured 299 times to look at the effect of repeated captures on body condition. One hundred nine bears were captured once only, whereas 98 bears were captured 2–10 times (Fig. 4b). Overall, juvenile males were captured most often (102 captures) and adult females with dependent offspring least often (28 captures). Multiple AIC_C models were supported, with the 4 most-supported models ($\Delta AIC_C \leq 2$) all including capture-effect terms (Table 3b). The highest-ranked model (model 1) indicated that BCI values varied as a function of sex and reproductive class, age, number of times captured, and interactions between sex and reproductive class and year, age and year, and number of times captured and year.

As with grizzly bears, mean BCI values for black bears generally increased with age in all reproductive classes, and rate of increase was similarly affected by number of times a bear was captured (Fig. 5b). The difference in mean predicted BCI value between a 15-year-old bear captured once and a 15-year-old bear captured 5 times was 0.73 for females and males and 0.57 for females with dependent offspring, which is equivalent to differences in body mass of approximately 14% for female and male black bears and 11% for females with dependent offspring (Cattet et al. 2002). The difference in body mass when captured 3 times was approximately 7% in all sex and reproductive classes.

To determine if a black bear's body condition affected its probability of being captured, we used the most-supported biological covariate model (model 1 from Table 1b) with BCI added as a covariate for recapture rate to estimate a slope coefficient for the relationship between recapture rate and BCI, that is, S(SEX) p(AGE + BCI) r(.) F(.). The estimated logit-scale slope was -0.042 ($SE = 0.18$, 95% $CI = -0.38$–0.30), suggesting a negative relationship between recapture rate and BCI. However, we considered the relationship insignificant because, similar to the grizzly bear analysis, a slope of zero was within the confidence interval.

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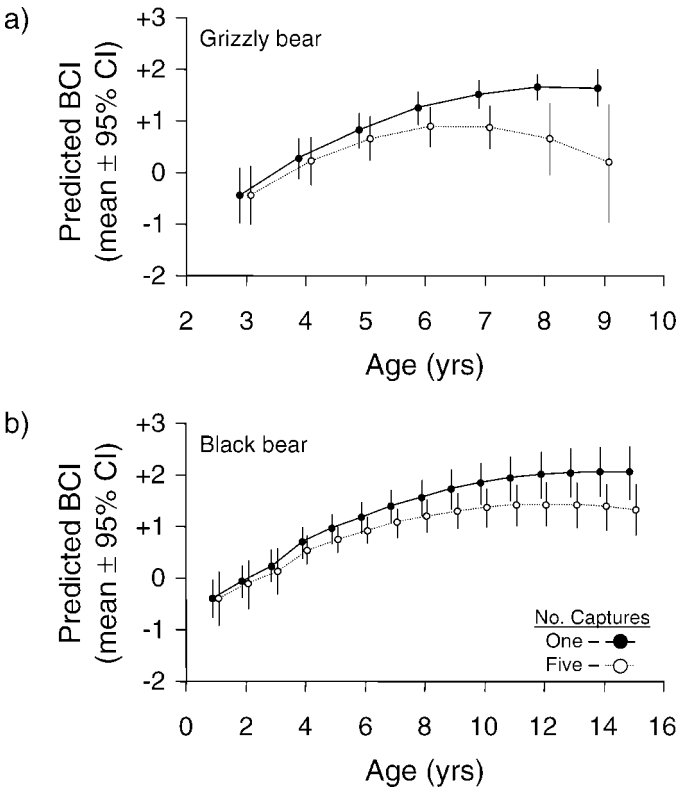


Fig. 5.—The relationship between body condition index (BCI) of a bear and its age as a function of number of times it was captured (once or 5 times) over the course of its lifetime predicted from the most-supported model for each species in Table 3. The analyses are based on capture records and BCI values for 130 grizzly bears captured 241 times and 207 black bears captured 299 times. The plots are standardized for a) male grizzly bears captured for the Foothills Model Forest Grizzly Bear Research Project in western Alberta, Canada (1999–2005), and b) male American black bears captured for the Pisgah Bear Sanctuary Black Bear Research Project in North Carolina (1981–2002). Although the age range for black bears (1–14 years) corresponds with the range of ages measured in captured male black bears, the age range for grizzly bears has been truncated at 9 years so that the total time interval of 6 years corresponds to the duration of sampling for this project, that is, 1999–2005. Ideally, we should have shown predicted curves for all levels of multiple captures (2–10) encountered in this study but this would have caused confusion and obscured any distinction with the curve for predicted BCI of bears "captured once only." We chose instead to show predicted curves for bears captured 5 times because this level was approximately midrange for number of captures per individual grizzly bear (2–8) and black bear (2–10). However, because capture effect is directly proportional to number of times captured, one can interpolate that curves for capture levels from 2 to 4 fall between predicted curves shown in the figure and curves for capture levels > 5 fall below the curve for "captured 5 times."

Discussion

We conducted a retrospective study using standard types of data (serum biochemistry, radiotelemetry, capture–recapture, and body condition) collected in many conservation-oriented studies involving carnivores. Our goal was to evaluate whether long-term ($\geq$1 month) effects of capture and handling were detectable and, if so, to identify possible implications this could have for the welfare of released animals and the interpretation of research results. Our analysis of data collected from 2 independent studies involving 2 species of bears, in geographically distinct areas, suggest that capture and handling affected study animals for a much longer duration than has been recognized generally. Specifically, we found evidence that: capture caused significant muscle injury in some bears, especially when captured by leghold snare; movement rates of many bears were affected for weeks after capture; and body condition of bears was negatively affected by capture, an effect directly proportional to the number of times a bear was captured and more evident with age.

Capture-related muscle injury.—Based on serum muscle enzyme (AST and CK) values from captures of 213 grizzly bears and 172 American black bears, we conclude that significant capture-related muscle injury (i.e., enzyme levels above reference interval values for captive bears) was indicated in samples collected from 102 grizzly bears captures and 134 black bear captures. Further, we believe extreme AST values (>5 times upper reference limit) measured in samples from 7 (6%) grizzly bears and 29 (18%) black bears captured by leghold snare were consistent with the occurrence of exertional (capture) myopathy, a noninfectious disease of wild and domestic animals characterized by damage to skeletal and cardiac muscles and associated with physiological imbalances following extreme exertion, struggle, and stress (Bartsch et al. 1977; Williams and Thorne 1996). Although AST in serum can originate from tissues other than muscle (e.g., liver and red blood cells), its strong positive correlation with concentrations of CK and myoglobin in grizzly bears, and with concentrations of CK in black bears, suggest that it was derived mostly from muscle.

Because serum concentrations of some blood constituents, including muscle enzymes, can be influenced by capture and handling, reference intervals for normal values are difficult to determine in wild species. As an alternative, we used reference intervals for captive grizzly bears and black bears (Teare 2002) as a frame of reference for comparison of muscle enzyme concentrations. Observation that serum muscle enzyme levels in wild black bears immobilized remotely by using drug-filled darts mounted on radiocollars (Powell 2005) are similar to those of captive black bears (mean ± *SD*; wild versus captive: AST—85 ± 15 U/liter versus 101 ± 52 U/liter; CK—133 ± 34 U/liter versus 163 ± 129 U/liter) corroborates comparisons between wild and captive counterparts. In our study, serum AST values in grizzly bears exceeded the upper limit of the reference interval for captive grizzly bears in 48% of samples measured, with the highest value (1,665 U/liter) at 12 times the upper limit, and serum CK values exceeded the upper limit of the reference interval in 40% of samples measured, with the highest value (37,280 U/liter) at 96 times the upper limit. Serum AST values in black bears exceeded the upper limit of the reference interval for captive black bears in 55% of samples measured, with the highest value (5,340 U/liter) at 26 times the upper limit, and serum CK values exceeded the upper limit of the reference interval in 78% of samples measured, with the highest value (109,780 U/liter) at 261 times the upper limit.

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Muscle injury associated with capture and handling is the most likely explanation for these differences, a conclusion supported by findings from this and previous studies (e.g., Hellgren et al. 1989; Huber et al. 1997) that confirm that method of capture affects muscle enzyme levels. In general, capture by leghold snare is associated with higher levels of muscular exertion and injury than capture by helicopter darting or barrel trap (Cattet et al. 2003b; Powell 2005). For both species in our study, AST and CK concentrations in serum samples collected from bears captured by leghold snare exceeded the upper limit of reference intervals in greater proportion and magnitude than measured in samples collected from bears captured by other methods.

Serum levels of CK, AST, and myoglobin released from damaged muscle are used to assess occurrence and severity of muscle injury in human and veterinary laboratory medicine (Singh et al. 2005; Williams and Thorne 1996). These measures, however, provide only a ''rough'' indication of the extent of muscle fiber destruction; their accuracy as markers of muscle injury is constrained by the fact that serum concentrations reflect the net outcome of 2 dynamic opposing processes—leakage from damaged muscle and clearance from blood circulation. Nevertheless, there is ample evidence from other studies to suggest that muscle injury was significant, if not severe, in some grizzly bears and black bears based on comparisons of the magnitude of difference between measured values and upper limits for reference intervals. If we consider AST levels, we recorded values ingrizzly bears as much as 12 times the upper limit, and in black bears as much as 26 times the upper limit. By comparison, roe deer (*Capreolus capreolus*) that died of capture myopathy had 3- to 4-fold increases in serum AST level at 6–9 h after capture (Montané et al. 2002); red foxes (*Vulpes vulpes*) with exertional myopathy caused by capture with unpadded leghold traps had AST levels 13- to 16-fold greater than levels measured in free-ranging foxes shot as controls (Kreeger et al. 1990); horses (*Equus caballus*) with severe hind-limb muscle injury (Dabareiner et al. 2004) or severe diaphragmatic necrosis (Valentine et al. 2002) had 3- to 24-fold increases in serum AST level; and children with limbs crushed during an earthquake had 20- to 26-fold increases in mean serum AST level depending on whether 1 limb or multiple limbs were crushed (Dönmez et al. 2001). In addition to comparisons with published data, we also confirmed diagnosis of severe exertional myopathy in a grizzly bear that died 10 days after capture by leghold snare (Cattet et al., in press). Its serum AST concentration at capture (894 U/liter) was 6 times the upper limit of the reference interval for captive grizzly bears.

We suspect that factors contributing to the development of exertional myopathy in snared bears are similar to those identified for other species (Williams and Thorne 1996), primarily extreme stress induced by capture and extreme exertion while struggling to escape the snare. Nonetheless, we have no evidence to suggest that this condition is a direct cause of long-term mortality in bears. Analysis of survival rates in this study suggested that probability of survival for some grizzly bears decreased when AST levels were high, but the effect was weak, with confidence intervals at different AST values overlapping and the confidence interval around the mean probability of survival increasing as serum AST level increased (Fig. 2). We interpret these results to indicate that exertional myopathy may affect survival of some grizzly bears, but if it does, it is more likely as a consequence of altered behavior leading to increased vulnerability to death by hunting or poaching, or less success at acquiring resources (e.g., food and shelter), than as a direct result of adverse physiological effects, for example, circulatory collapse. We have no explanation for why high AST levels had no significant effect on survival of black bears in our study, even though a larger fraction (18% versus 6%) of those caught in snares had extreme values of AST consistent with exertional myopathy.

After muscle injury, increased concentrations of CK and myoglobin persist only a day or two (Lappalainen et al. 2002), and of AST as long as 5–7 days (Krefetz and McMillin 2005; Latimer et al. 2003), unless the injury is progressive. In our study, we found no evidence of persistently high (or low) serum AST, CK, or myoglobin concentrations in bears captured multiple times. Even in grizzly bears and black bears captured 2 or 3 times within periods ranging from 1 to 3 weeks, serum AST, CK, and myoglobin concentrations appeared mostly to reflect method of capture, being high when captured by leghold snare and lower when captured by helicopter darting or barrel trap. Although increases in serum muscle enzymes and myoglobin are short-term after muscle injury, the duration required for injured muscle to heal and for muscle function to return to normal is considerably longer. With minor injury, skeletal muscle can repair and regenerate within 4–8 weeks (Hill et al. 2003; Schneider-Kolsky et al. 2006). With more severe or extensive injury, pathologic changes to muscle structure (necrosis, mineralization, and atrophy) can affect strength and range of motion for a much longer duration (Porzio et al. 1997; Ross et al. 1999).

Mobility after capture.—Immediately after capture, movement rates of grizzly bears and American black bears were reduced for 3–6 weeks before returning to mean levels. Although numerous studies have investigated potential effects of capture on use of space by radiocollared animals (e.g., Chi et al. 1998; Moa et al. 2001; Windberg and Knowlton 1990), we are aware of only a few studies that have looked at movement rates in relation to capture and handling. Amstrup and Beecham (1976) and Craighead and Craighead (1972) concluded that the impact of research activity on daily movement rates of black bears and grizzly bears appeared to be negligible in their respective studies. We found, however, that sensitivity of detecting differences in movement rates of black bears diminished quickly as the interval between location fixes increased, a finding that underscores an advantage of the greater temporal resolution of GPS collars over conventional VHF transmitters, as has been described by others (Obbard et al. 1998; Schwartz and Arthur 1999). Consequently, Amstrup and Beecham (1976) and Craighead and Craighead (1972) may not have detected changes in movement because of long intervals between location estimates.

Our analysis identified that movement rates of bears also were influenced by month of year, day of month, and

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reproductive class of bear. Other studies have shown that different reproductive classes move at different rates, especially during the spring breeding season when male grizzly and black bears move at greater rates than do females (Amstrup and Beecham 1976; Ballard et al. 1982; Powell et al. 1997). This has been explained as movements of females reflect efforts to secure food sources, whereas movements of males maximize overlap with home ranges of females (Powell et al. 1997; Rogers 1987). Daily movement rates of grizzly bears in our study differed by day of month as well as by month. A plausible explanation for this interaction between day and month is that the grizzly bear study involved animals inhabiting home ranges across a wide elevational gradient (>1,600 m). Between extremes of home ranges in alpine versus low-elevation agricultural areas, differences in local climate (e.g., precipitation and snowmelt) and plant phenology likely affected movement rates of grizzly bears in different ways at different times (Munro et al. 2006). This was especially evident during April and May when snow was still plentiful at higher elevations and bears remained in or near dens, but at lower elevations snow was scarce and bears were moving in search of food. In general, through consideration of these biological and environmental factors and their potential interactions in our models, we were able to account for more bear-to-bear variation in movement rates and increase the power of the analyses to detect capture effects.

Severity of muscle injury, as reflected by serum AST concentrations, affected movement rates of grizzly bears and black bears. However, this effect was evident only in bears with AST levels > 3 times the upper limit of the reference interval. Movement rates also were depressed in bears with low AST levels but this likely was caused by factors other than muscle injury, because the prolonged effect of capture on movement rates occurred in many bears irrespective of capture method used. This finding warrants more detailed investigation of specific and cumulative effects of other stressors that bears may be exposed to during and after capture, for example, sample collection, marking, and carrying radiotransmitters.

Body condition and repeated captures.—The finding that capture and handling affected movement rates for a prolonged period in many bears prompted us to question whether alterations in movement rates could in turn affect assimilation and use of stored energy. As a measure of stored energy, we used a BCI developed for bears that correlates well with the combined mass of fat and skeletal muscle in a bear relative to its body size (Cattet et al. 2002). Because it is not possible to calculate a BCI value for a bear without 1st capturing it, we compared body condition in bears captured once only or captured the 1st time (the control group) to body condition in bears captured repeatedly (≥2 times; the treatment group). We hypothesized that capture and handling affected changes over time in body condition of bears in a negative manner, and the effect would be proportional to the number of times a bear was captured. An implicit assumption in this analysis was that bears captured once and bears captured repeatedly would show similar relationships between body condition and age in the absence of captures. In other words, bears captured repeatedly also were a random sample of the population. This assumption was supported by the fact we were unable to confirm a significant relationship between BCI values for individual bears and their probability of being captured (or recaptured).

We found that body condition in both species tended to increase with age, but rate of change was inversely proportional to number of times a bear was captured, that is, the more often a bear was captured, the lower its age-related rate of change in body condition. Further, this effect became more apparent with age. When translating BCI values into body mass (kg) and comparing between adult bears captured 3 times versus bears of the same age and length captured once, we found a difference in body mass of approximately 14% in grizzly bears and 7% in black bears, and when comparing with bears captured 5 times, a difference in body mass of approximately 25% in grizzly bears and 11–14% in black bears. The significance of a greater effect on grizzly bears is uncertain given that a model without capture effects (model 5 in Table 3a) was marginally supported by our analysis ($\Delta AIC_C = 2.04$). Nevertheless, we conclude that a long-term consequence of capture and handling for both species is a reduction in energy storage and the magnitude of this effect increases with the number of captures. We suggest that this effect may occur because either energy intake is decreased (e.g., reduced foraging), or energy use is increased (e.g., healing of injured tissues), or a combination of both.

The negative effects of capture and handling on body condition have potential, in turn, to affect reproduction and lean body growth negatively, especially in bears captured multiple times. The relationships between body condition and these biological functions have been examined in many mammals (Boltnev et al. 1998; Gittleman and Thompson 1988), including grizzly bears (Stringham 1990b), black bears (Samson and Hout 1995; Stringham 1990a), and polar bears (*Ursus maritimus*—Atkinson and Ramsay 1995; Atkinson et al. 1996). Among bears, solitary adult females that enter dens in autumn in poor body condition are least likely to be seen with offspring the following spring. For those that produce cubs successfully, litter weight at den emergence is dependent upon their body condition in the previous autumn (Atkinson and Ramsay 1995; Samson and Hout 1995). Individuals with better body condition produce heavier cubs. For polar bears, heavier cubs are more likely to survive their 1st spring to summer period on the sea ice (Ramsay and Stirling 1988) and, in the case of females, are more likely to become large adults (Atkinson et al. 1996). We expect that heavier grizzly and black bear cubs also survive better.

Implications for wildlife welfare and research.—Although our findings have important implications for researchers and management agency personnel involved in the capture and handling of bears, we believe they are also pertinent to the conservation, research, and management of other wild carnivores. Indeed, methods of capture we used and types of data we collected are common to many research programs. It seems plausible that different species also will respond similarly when faced with similar stressors. This possibility should at the very least challenge persons capturing wild animals to evaluate their capture procedures and research

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results carefully. Without this effort, one cannot conclude with any certainty that capture effects are negligible.

A welfare implication of this study concerns use of leghold snares, a method of capture used commonly for ursids, but also for other wild carnivores, especially canids and felids. Our findings show that capture by this method relative to capture by helicopter darting and barrel traps is more likely to cause significant muscle injury (serum muscle enzyme levels $>$ reference values), and in some cases exertional myopathy (serum muscle enzyme levels $>$ 5 times reference values). Further, high serum levels of muscle enzymes detected in American black bears captured by leghold snare in this study suggest that use of cushioning devices, such as automobile hood springs, may not reduce severity of muscle injury or risk of exertional myopathy. Obviously, need exists to modify application of this method to reduce injury or to develop safer capture techniques that are as effective and practical as leghold snares. Use of trap-monitoring devices that signal when a bear is captured, therefore minimizing restraint time, may help reduce capture-related injury and enable researchers to determine duration of restraint (Larkin et al. 2003). Use of motion-activated video cameras at trap sites would allow researchers to assess animals' reactions to capture, which could potentially aid in development of better snaring techniques by illustrating how injury occurs, and how injury may be avoided. In parallel with developing and improving traps, there is also need to develop sensitive techniques to detect and evaluate injury on-site before a captured animal is released. Analysis of serum biochemical markers, as was done in our study, is of limited use because of the delay between collection and analysis of blood.

Another welfare implication is the potential negative effect of multiple captures of individual animals on body condition. As body condition fades, so too does an animal's potential for growth, reproduction, and survival. Clearly, researchers need to find ways to minimize occurrence of repeated captures of individual animals and for mark–recapture–type study designs where repeated sampling is required, explore the feasibility of less invasive approaches than animal capture, for example, DNA hair census.

A research implication of this study is that failure to recognize and account for long-term effects of capture and handling can potentially confound results leading to erroneous interpretations. For example, descriptions of activity patterns or determination of home ranges may be inaccurate if time elapsed after capture is not considered as a potential factor in analysis of movement rates or locations. Similarly, interpretation of body condition trends in association with environmental variables (e.g., measures of habitat quality) may be incorrect if number of times an animal is captured is not also considered in analyses as a potentially confounding factor.

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