Behavioral and physiological responses of American black bears to landscape features within an agricultural region

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Abstract. Human activities and variation in habitat quality and configuration have been shown to influence space use patterns in many species, but few studies have documented the physiological responses of free-ranging animals to these factors. We combined remote biologger technology, capturing continuous heart rate values, with locational data from GPS collars to investigate the behavioral and physiological reactions of American black bears (Ursus americanus) to a landscape dominated by agriculture (52.5% areal cover). Our study occurred at the edge of the range of this species, with small, scattered patches of forest within a mosaic of crop fields and an extensive road network. However, only ~2–4% of the area contained crops that bears consumed (corn, sunflowers, oats). We used GPS locations to identify the habitat that bears occupied, and to estimate their rates of travel. Heart rates increased with movement rates, rising by over 30% from resting rate to their fastest travel speeds. We used a modeling approach to distinguish among factors that influenced heart rates independent of movement rates. Bears commonly crossed agricultural areas that provided no food or cover and their heart rates, elevated beyond what was expected from their movement rate, were indicative of a stress response. However, when bears entered agricultural areas composed of edible crops, many individuals showed reduced movement and slower heart rates, suggesting that bears foraging there felt at ease or crops allow bears to more easily forage due to their dense spatial arrangements. Unexpectedly, female bears elicited lower heart rates and lower levels of activity in the most fragmented patches of natural habitat, possibly a sign of human-avoidance behavior or a reaction related to crossing roads. During fall, as bears prepared for hibernation, their heart rates declined two weeks before their movements slackened, evidence that metabolism slowed to enhance fat accumulation; they also shifted to a nocturnal activity pattern, likely to reduce exertion during the heat of the day. The use of a physiological monitor provided new insights on bear biology and ecology that would not have otherwise been apparent.

Key words: biologger; crops; GPS; habitat fragmentation; heart rate; landscape; metabolism; Minnesota; movement; physiology; stressors; Ursus americanus.

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INTRODUCTION

Understanding the relationship between an organism and its natural environment is fundamental to addressing many questions in applied and theoretical ecology (Brown et al. 2004, Costa and Sinervo 2004). Telemetry studies have increased our understanding of how various organisms interact with their environment by providing locational information on free-roaming individuals. However, our relative knowledge concerning physiological responses of organisms to stimuli in their natural habitat is lacking, often because most studies of physiology are confined to laboratory settings. In contrast to other visible measures of health (e.g., weight loss, illness, population decline), physiological measurements can capture more immediate changes to an organism’s health and thus provide an early warning system for deleterious influences in a changing environment. Advances in biologger technology, which can remotely measure physiological parameters, can be combined with locational data to examine physiological responses to intrinsic and extrinsic factors over extended time periods and in natural settings (Cooke et al. 2004b, Block et al. 2005).

Recently, much research has been focused on determining how landscape configuration (Ellis et al. 2011) and habitat types (Huey 1991, Homyack 2010) may in turn influence innate physiology. For example, heart rate (HR) measurements can provide an indirect measure of field metabolic rates (Butler et al. 2004) and when connected with locational data to examine physiological responses to intrinsic and extrinsic factors over extended time periods and in natural settings (Cooke et al. 2004b, Block et al. 2005).

In recent decades, American black bear (Ursus americanus) populations have been expanding geographically (Scheick and McCown 2014), and in the process have come into greater contact with human-occupied or modified landscapes; their interaction with these landscapes has thus far been measured in terms of altered activity patterns (Beckmann and Berger 2003a, Baruch-Mordo et al. 2014), diets (Jonker et al. 1998), habitat use (Obbard et al. 2010, Merkle et al. 2013) and survival (Beckmann and Lackey 2008, Van Manen et al. 2012). This species is highly mobile, enabling access to spatially varying resources (Garshelis and Pelton 1981, Noyce and Garshelis 2010). Black bears are also relatively human-tolerant and take advantage of anthropogenic food resources (Maddrey and Pelton 1995, Garshelis et al. 1999). In Minnesota, USA, black bears recently expanded into an agriculturally dominated region in the northwestern corner of the state and exploited crop fields ( Ditmer 2014). Here, bears range over especially large areas ( Ditmer 2014) and are exposed to a variety of habitat types, levels of human influence, and forage options, making this an ideal site to examine physiological effects of the environment.

Here we describe the combined use of GPS collars and cardiac monitors to provide unique insights as to how bears react to a human-altered habitat at both physiological and behavioral levels. This investigation involved the portion of the year when bears were actively moving around the landscape, whereas most previous physiological measurements of bears focused on the denning period (Nelson et al. 1983, Laske et al. 2010, Laske et al. 2011). Our first objective was to quantify the influence of movement on heart rate. We hypothesized that a bear’s HR will increase with faster movement speeds. Second, we compared seasonal changes in the relationship between movement and HR over the course of the active period of the year. We hypothesized that the relationship would change seasonally with activity patterns (Amstrup and Beecham 1976, Garshelis and Pelton 1980), especially in the fall during hyperphagia (a period of intense caloric intake and consequent fat gains prior to hibernation). We posited that bears follow a similar pattern to that found in small hibernators in which metabolic rate diminishes prior to...
reductions in food intake, enabling significant gains in body mass (Florant and Healy 2012).

Our third objective was to discern the effects of anthropogenic features (e.g., roads, crop fields, habitat fragmentation), habitat type, weather, and temporal factors (season and time of day) on bear behavior and physiology. These can influence HR either directly or indirectly, by causing changes in movement rates. We predicted that habitats with different food density and understory density (i.e., obstruction to movement) would have distinct effects on their heart rates. We expected that roads, highly fragmented habitat, and agricultural fields would increase heart rate and movements of bears, as they have been shown to increase movement rates in other species (MacArthur et al. 1979, Coffin 2007, Dussault et al. 2007). We predicted that this effect would be gender-specific, as males tend to encounter these features more often due to their larger home ranges (Powell et al. 1997) and their tendency to be less risk-averse (Beckmann and Berger 2003b, Ditmer 2014). Finally, we hypothesized that heart rates would increase, but movement rates would decrease, when bears encountered high temperatures (Speakman et al. 2003, Zub et al. 2009), winds or other extreme weather events (Wingfield et al. 1998, Theil et al. 2004). Our novel use of new biologger technology, coupled with routinely deployed GPS collars, provided a unique opportunity for enhanced understanding of bear behavioral and physiological relationships with their environment.

**Materials and Methods**

**Study area**

Northwestern Minnesota marks the western edge of the eastern population of the American black bear (Scheick and McCown 2014). Agricultural crops in this area attracted large numbers of bears during a statewide failure of wild bear foods in 1995, and bear numbers have remained high and growing ever since, even while statewide bear numbers have declined (Fieberg et al. 2010, Garshelis et al. 2011). The landscape of northwestern Minnesota is comprised of agricultural fields and small woodlots with a few larger areas of state and federal land. A majority of the landscape is dedicated to agricultural production (52.5%), primarily soybeans and wheat with small amounts of corn, oats and sunflowers (collectively ~2–4%, varying by year). A total of 17.3% of the landscape is forested, comprised mainly of aspen/white birch (Populus tremuloides/Betula papyrifera, 12.9% of the total area) and bur oak (Quercus macrocarpa, 3.6% of the total area). The region was once below glacial Lake Agassiz and the resulting flat landscape has many areas that are poorly drained, at least seasonally, and covered by lowland shrub (11.5%, primarily willow Salix spp., alder Alnus spp., red-osier dogwood Cornus sericea), wetlands (11.2%), and grasslands (7.4%, Conservation Reserve Program land, temporarily fallow fields, or remnant prairie). Urban areas make up a small percentage of the total land cover (0.2%), but the road network is extensive (0.55 km road/km²).

**Animal location and heart rate data**

During the summer of 2007–2011, we captured bears in baited barrel traps, and fit them with either store-on-board GPS devices (Telemetry Solutions, Concord, CA, USA) or GPS collars that relayed fixes via the Iridium satellite system (Vectronic Aerospace, Berlin, Germany). We visited all collared bears in winter dens to change or refit collars, download stored GPS data, obtain morphometric and physiological measurements, and check on their general health status. We programmed GPS collars to collect fixes at 1–6-hour intervals, depending on the model of collar and time of year. Locations were accurate to within 15–25 m. Vectronic collars were also equipped with activity sensors that recorded acceleration on the X-Y axis during collar deployment.

During den visits in 2008–2013, we surgically implanted cardiac monitors developed for humans (Medtronic Inc., Reveal XT Model 9529, Minneapolis, MN, USA; specifications: nine cc; 8 mm × 19 mm × 62 mm; 15 g). Monitors were sterilized in ethylene oxide and inserted subcutaneously in a peristernal location using aseptic techniques. Monitors provided two data points per day, representing the average HR during daytime (08:00–20:00) and night-time (00:00–04:00) hours throughout the year (henceforth night or day HR interval). These two HR intervals were of different duration, and excluded eight hours per day, a constraint stemming...
from the intended use of these devices in humans. Data were downloaded noninvasively during subsequent winter den visits using transcutaneous telemetry (CareLink Model 2090 Programmer with software Model SW007, Medtronic; details in Laske et al. 2011). All methods and animal handling were approved by the University of Minnesota’s Institutional Animal Care and Use Committees (1002A77516).

**Measured variables**

We created two data sets for analysis using the same measured variables. The first, which we analyzed to discern factors affecting movement rate, included all GPS locations from all hours of the day, each as a separate record. The values associated with each location or movement step were modeled for relationships to bear movement rate (see section: Movement rate models). In the second data set, which we used to discern effects on HR (including the effect of movement speed), we partitioned the data into daily day/night intervals that were aligned with HR intervals and used the average values of any variable measured more than once across that interval (see section: Heart rate models).

Accordingly, we estimated movement rate (MOVEALL, meters/hour) by dividing measured step lengths (i.e., straight-line distances between consecutive GPS observations) by the time-interval between locations for any locations occurring within six hours of one another. We created a second movement variable that averaged movement speeds within HR intervals (MOVEHR) for use in HR analyses. For this variable we included GPS locations from one hour before and after the HR intervals for store-on-board GPS units because these units had lower fix success than the Iridium satellite collars.

We used ArcMap 10.1 (Environmental Systems Research Institute, Redlands, CA, USA) to overlay GPS locations onto a GIS land-cover layer (Minnesota Department of Natural Resources 2012). We classified locations as occurring within one of six composite cover types: (1) aspen-dominated forest (ASPEN: aspen, birch, black ash, *Fraxinus nigra*), (2) oak (OAK: bur oak, upland shrub), (3) marsh (WET: aquatic and marsh), (4) lowland shrub (LLS: lowland deciduous and coniferous shrubs), (5) grassland (GRASS) or (6) agricultural (AGFIELD) fields comprised of crops not commonly consumed by bears (e.g., soybeans, wheat). We added another covariate for distinguishing locations in three types of crops that bears consumed—corn, oats or sunflowers (CROP); this distinction was based on year-specific cover maps created by the United States Department of Agriculture, National Agricultural Statistics Service (United States Department of Agriculture 2012; http://www.nass.usda.gov/). We classified land-cover types as anthropogenic (agricultural, urban, roadsides) or natural (all other classifications). We used the Minnesota Department of Transportation (2012) map of roads to buffer an anthropogenic swath of habitat 25 m to each side.

For each bear GPS location, we calculated mean patch size (km$^2$) for natural habitats, distance (m) to the nearest edge of a patch of natural habitat and distance to the nearest road. We recorded patch size and distance to edge as zero for locations in agricultural areas or the roadway buffer. We created a metric of habitat fragmentation (FRAG) using the first axis of a principle component analysis (PCA) that combined patch size, distance to habitat edge and distance to road using the following formula: 

$$
FRAG = -0.532 \times \text{(patch size)} - 0.596 \times \text{(distance to edge)} - 0.601 \times \text{(distance to road)}.
$$

Larger values of FRAG were indicative of bear locations in areas with small habitat patches, distances closer to habitat edges or roadways. We created a road crossing variable (ROADX) by counting the number of roads crossed over a movement path of connected consecutive locations. We considered all road types the same because bears often crossed multiple roads during a HR interval and only a few higher traffic highways bisect the study area.

We created kernel density estimators of home range using least-squares cross-validation to create isopleths (5–100%) of annual locations for each bear-year (Geospatial Modeling Environment; Beyer 2012). We overlaid each GPS location on to the underlying isopleth boundaries (ISO) and assigned each location the corresponding ISO value. Smaller values for ISO represent locations within the most-used part of each home range. We used the average ISO values associated with each HR interval when analyzing heart rate and the ISO value associated with the final location of each movement step was used when
analyzing movement rates.

We used the pheno package in program R (Schaber 2012, R Core Team 2013) to assess photoperiod (PHOTO). We converted all dates to Julian (JULIAN), and for analyses including HR, we created a variable to match the day or night HR interval (DAYNITE). We created a variable (LIGHT) to categorize each hourly increment in the day as either before or after sunset (“sun” or “moon”; movement analysis only).

We obtained weather data from weather stations in Gatzke and Thief River Falls (http://www.wunderground.com/), Minnesota. We utilized data including daily maximum, minimum, and mean temperatures (degrees Celsius, MAX-TEMP, MINTEMP, MEANTEMP); maximum and mean humidity (% relative humidity, MAXHUMID, MEANHUMID); total precipitation (cm, PRECIP); average level of cloud cover (0–10, CLOUD); average wind speed (mph, WIND); and a binary value for thunderstorm events (TSTORM).

**Modeling approach**

We created separate models for assessing the influence of measured covariates on movement rate and HR to better understand direct and indirect effects on bears’ HR’s. We hypothesized that movement rate would have a strong positive influence on HR, so variables affecting movements necessarily had indirect effects on HR. We also sought to identify factors that directly influenced HR, after we controlled for movement rate (MOVEHR) by including it as a predictor.

We used a two-step modeling approach: (1) first we fit models to individual bear-years using a stepwise selection process; then (2) we fit a mixed model to all the data, including only those covariates supported by at least four individual bear-year models. Our decision to first create models for each bear-year was a conservative choice due to the large number of degrees of freedom associated with fitting mixed models using all variables and all bear-years. Step two allowed us to test a subset of the variables using the full dataset of bear-years, while also allowing for random coefficients (i.e., coefficients specific to each bear-year).

Covariates representing natural and anthropogenic landscape attributes were modeled differently for movement and HR models. In the HR model, we constructed covariates using the proportion of GPS locations occurring within each habitat type during the HR intervals. For example, the OAK variable was assigned the percentage of GPS locations that occurred in oak habitat during the given HR interval. In the movement model, we created binary covariates to represent the cover type associated with the last GPS location of each movement step. We divided ROADX by the number of hours in a HR interval for HR models and divided ROADX by the number of hours in a movement step for movement models.

Before fitting models we checked for collinearity among measured variables using variance inflation factors (VIF, Kutner et al. 2005). If two variables caused a large increase in VIF (10+), we chose the most biologically appropriate to include in analyses (Table 1).

**Heart rate models**

We created model sets for each bear-year by regressing average HR in beats per minute (bpm) as a function of: (1) movement rate (MOVEHR, m/h), (2) temporal variables (DAYNITE, splines based on JULIAN), (3) weather conditions (TEMP, WIND, PRECIP, CLOUD, TSTORM), (4) percentage of habitat use by habitat type (OAK, LLS, GRASS, MARSH), (5) road crossings per hour (ROADX), (6) degree of habitat fragmentation (FRAG), (7) location within the home range (ISO), and (8) percentage of time spent in agricultural (AGFIELD, not used for bear foraging) and crop fields (CROP, consumed by bears: corn, sunflowers and oats; Table 1). We expected bears to respond differently to roads and habitat fragmentation, depending on time of day since bears may be less stressed when moving through these areas in the dark so we included interactions for ROADX × DAYNIGHT and FRAG × DAYNIGHT. Bears are known to seasonally change activity patterns, so we included the interaction DAYNIGHT × splines for JULIAN. We also hypothesized that the relationship between HR and ambient temperature as well as HR and agricultural areas might change seasonally so we tested the interactions MEAN-TEMP × splines for JULIAN and AGFIELD × splines for JULIAN. Incorporating splines based on JULIAN allowed us to include a piecewise polynomial function to account for changes in the
HR or the relationship between a covariate and HR over time (when considering interactions).

We fit models using generalized least squares (GLS) to allow for temporally autocorrelated residuals via the gls function in the nlme package of program R (Pinheiro et al. 2013, R Core Team 2013). We used regression splines with five degrees of freedom when modeling the effect of JULIAN, to allow for nonlinear seasonal trends in HR. Incorporating interactions with JULIAN, modeled in this way, also allowed the effect of covariates on HR to vary over time. Additionally, we explored the seasonal changes in heart and movement rate data by fitting loess curves to the data based on Julian date. We excluded day or night periods with inadequate data to calculate movement rate. We accounted for autocorrelation among HR averages by including a first order autoregressive correlation structure (AR1). For this purpose, we started at the first HR interval in each bear-year and created a count of HR intervals as discrete units, skipping periods that were excluded due to insufficient data. We included CROP in individual bear-year models if >5% of HR intervals included at least one observation in CROP.

For each set of models, we used backwards stepwise elimination to remove the least significant covariates. We considered covariates with $p \leq 0.05$ to be significant. If a covariate had a $p$ value near this threshold, we looked at its effect on the residuals and the magnitude of influence on the predicted response to determine if it should be included in the model.

**Movement rate models**

We modeled log-transformed movement rate (MOVEALL, m/hour) for each season and bear-year as a function of a cyclic smoother (cubic regression splines where the ends must meet, Wood 2006) based on: (1) HOUR of the day, (2) habitat types including agricultural fields (HAB-...
ITAT), (3) whether the agricultural area contained potential bear forage (CROP), (4) habitat fragmentation (FRAG), (5) road crossings per hour (ROADX), (6) weather conditions (TEMP, WIND, PRECIP, CLOUD, TSTORM), and (7) location within the home range (ISO). We included an interaction between SUN × ROADX because we hypothesized that bears might interact with roads differently at night (Table 1).

We used generalized additive models (GAM) in program R with package mgcv (Wood 2006, following Martin et al. 2013) to model spring (den exit in March or April to 1 July), summer (1 July to 1 September), and fall (1 September to den entrance in October or November) movement rates in separate model sets. We used GAMs to model non-linear relationships instead of regression splines as in the HR models, owing to the need for greater flexibility when modeling diurnal patterns instead of seasonal trends as modeled by the regression splines. We assumed errors followed an autoregressive correlation structure and used time (in minutes) since the first observation to account for this feature. We required 3% of locations within a season to be in the CROP classification for consideration in an individual’s model set, otherwise we assumed the bear was simply passing through the field and not foraging. We used the same process as the HR models to determine the best supported covariates for each bear-year model set.

**Mixed models**

The commonly supported covariates in the individual HR models were included in a linear mixed model fit using the lme function in the nlme package of program R (Pinheiro et al. 2013, R Core Team 2013). We used the commonly supported covariates in the individual movement models in a generalized additive mixed model (GAMM) in program R with package mgcv (Wood 2006) for each season. For both model sets, we used bear-year (BEARYEAR) as a random intercept and included a first-order autoregressive correlation structure, formulated in the same manner as in the GLS and GAM models. To incorporate individual variation in the relationship between movement and HR, we modeled movement rate (MOVEHR) as both a random (slope) and fixed effect in the HR model. To better account for differences between the sexes we considered additional interactions in the global model (e.g., HABITAT × SEX [movement model], FRAG × SEX × DAYNIGHT [HR model]). We initially fit mixed models using maximum likelihood during model selection process then refit the best-fitting model using restricted maximum likelihood to obtain unbiased parameter estimates (Zuur et al. 2009). We used the effects package (Fox 2003) to generate model-based predictions of the movement and HR values with associated 95% confidence intervals using the best-fitting models. We inspected relationships between individual covariates and the response variable, while holding all other covariates at their mean values, to assess a covariate’s strength of influence on predicted HR.

**Model validation**

To test the validity of our models, we repeated our analyses of HR and movement rate using three additional bear-years obtained in 2013. We fit our top HR model to the new data using the same mixed modeling methodology and compared the results with our significant findings from the data obtained between 2009 and 2012. We re-fit our HR mixed model utilizing all available data and reported updated results. We modeled the movement rates from the 2013 data using the same individual GAM models and compared the seasonal results with our previous significant findings.

**Post hoc analysis**

To further investigate what turned out to be an unexpected relationship between bear HR and landscape fragmentation (FRAG), we utilized data from activity sensors on seven bears (five female, two males) during 2012–2013. An activity value was reported every 5 minutes, from which we calculated an average activity value (ACT) for each HR interval. We modeled HR as a function of activity and movement (MOVEHR), again controlling for seasonal patterns by modeling JULIAN with regression splines. We also included a random intercept for BEARYEAR, and we used the same autocorrelation structure as in the other HR models. We included MOVEHR as a covariate in all models despite correlation with activity to discern any residual effects of activity on HR beyond locational movement. To allow for
the possibility of a FRAG × DAYNIGHT × SEX interaction, we fit separate models to males and females and for day and night HR intervals.

**RESULTS**

We obtained paired locational and HR data for seven different bears (three male, four female), representing nine bear-years (four males, four females with cubs, one solitary female) during 2009–2012. In seven bear-years, HR data spanned an entire year of activity (den emergence to den entry); mean number of monitored days was 172 (SE = 11, range = 118–221) and mean number of useable HR intervals for the nine bear-years was 308 (SE = 34, range = 169–439). For our movement analysis we incorporated an average of 1,868 (SE = 436, range = 446–3,658) movement steps per individual annually, 564 (SE = 126, range = 166–1,065) in the spring, 644 (SE = 138, range = 158–1,290) in the summer, and 743 (SE = 186, range = 68–1,520) in the fall.

Spring movement rates (MOVEALL, Fig. 1A) were low from sunrise through the middle of the day, increased rapidly near sunset for about 4 hours (19:00–23:00 h), then declined sharply in the hours approaching sunrise. Spring movements were slower and had less variation throughout the day than during summer or fall (range: spring: −0.5–1.0, summer: −1.5–1.5, fall: −1.0–1.0; Fig. 1). Trends around sunset and sunrise continued into summer, but bears became more active during daylight hours and movement rates reached the maximum values of any season (Fig. 1B). In fall, daytime activity greatly diminished, and bears returned to a diurnal movement pattern similar to spring, but with extended hours of activity after dark (Fig. 1C). Bears moved the least in the hours immediately pre-dawn in spring and summer, but in mid-day during fall.

HR and movement rate, both day and night, exhibited parallel seasonal trends from April–August (Fig. 2). From September to den entrance, however, as bears reduced activity prior to denning, HR fell earlier and more quickly than corresponding movement rates, particularly during the night (Fig. 2). The average HR started to decline 16 days earlier than movement rate (nighttime data: 5 September vs. 21 September). All individual bear-years, except the largest individual, exhibited this relationship (Fig. 3A–H). In some cases, movement rates increased even after HR started to decline for the season.

![Fig. 1. Influence of hour of day on log movement rate (MOVEALL, mean and 95% CI) during (A) spring, (B) summer, and (C) fall of American black bears in northwestern Minnesota, 2009–2012. Gray shaded areas represent the approximate range of sunrise and sunset. Original data were in meters per hour.](image)
Direct effects on bear heart rates

Movement rate (MOVEHR) positively affected HR for all bear-years and was significant in the mixed model ($\beta = 1.87$, SE = 0.35, $p < 0.001$; Fig. 4A). The best-fitting model included a random intercept for bear-year and a random slope for movement rate (likelihood ratio test, no random slope vs. random intercept: $L = 93.79$, $p < 0.001$).

Mean predicted HR was 21% higher for bears moving at 66 m/h (median movement rate) than at 0.1 m/h (slowest movement rate for a non-stationary bear) and 34% higher when moving at the fastest observed rate of 3.2 km/h (Fig. 4B).

After accounting for the influence of movement rate (MOVEHR) and the seasonally changing influence of the day-night cycle, bear HR
provided further information about bears’ responses to crop fields, habitat fragmentation, ambient temperature, and location within their home range (Table 2, Fig. 5). Both sexes were infrequently located in agricultural fields that did not contain corn, sunflowers, or oats (AGFIELD; $\bar{X}_m = 5.6\%$ of all locations, 95% CI: 2.4–8.7%; $\bar{X}_f = 4.7\%$, 95% CI: 0.0–8.3%). However, because these fields were the dominant feature on the landscape (areal coverage $\approx 48.5–50.5\%$) bears crossed them regularly ($\bar{X}_m = 42.6\%$ of movement steps, $\bar{X}_f = 26.1\%$). Conversely, despite being a small portion of the landscape ($\approx 2–4\%$), males were located in corn, sunflower and oat fields (CROP) frequently ($\bar{X}_m = 10.2\%$, 95% CI: 10.6–21.0%); females, however, rarely used CROP ($\bar{X}_f = 1.2\%$, 95% CI: 0–3.2%). Females moved across AGFIELD particularly quickly, whereas males did not (summer; Fig. 6B vs 6C). Movements across AGFIELD prompted higher than expected HRs in both sexes (Table 2, Fig. 6), whereas when bears were located in CROP, they tended to have lower or no greater than expected HR (three of five bear-years had significant negative relationships).

During the summer, female and male bears responded differently to landscape fragmentation: whereas movement rate of females declined, males moved more quickly within natural habitat with the highest levels of fragmentation (e.g., small patch of aspen forest surrounded by roads and agricultural fields); no other significant effects of FRAG on movements were apparent (Fig. 7). Additionally, HR was lower when bears used more fragmented portions of the landscape, but the significant interaction terms in this relationship suggested that the daytime HR of female bears showed the strongest response to FRAG (Table 2). Our post hoc analysis suggests that females’ unexpected HR response to FRAG,
Fig. 4A and 4B. (A) Influence of movement rate (MOVEHR, log(m/hour)) on heart rate (bpm, mean and 95% CI) of free-roaming black bears, based on the best-approximating population model with all other covariates held constant at their mean values. (B) Percent increase in mean estimated heart rate with quantile change in log movement rate. Original movement rate data were in meters per hour.

Table 2. Beta estimates, standard errors, t-statistics and p-values for the covariates included in the top linear mixed (population) model assessing factors influencing heart rate of American black bears in northwestern Minnesota (2009–2012, excluding time spent in the den).

| Type          | Covariates† ‡                                  | β      | SE(β)   | t      | p       |
|---------------|-----------------------------------------------|--------|---------|--------|---------|
| Intercept     |                                               | 40.050 | 3.663   | 10.934 | <0.001  |
| Movement      | MOVEHR                                        | 1.866  | 0.350   | 5.334  | <0.001  |
| Individual    | SEX: Male                                     | −9.113 | 2.707   | −3.366 | 0.012   |
| Temporal      | JULIAN S1                                     | 45.057 | 9.088   | 4.958  | <0.001  |
|               | JULIAN S2                                     | 12.868 | 7.126   | 1.766  | 0.078   |
|               | JULIAN S3                                     | 80.900 | 14.090  | 5.742  | <0.001  |
|               | JULIAN S4                                     | 9.627  | 8.162   | 1.180  | 0.238   |
|               | DAYNIGHT:Night                                | 3.700  | 1.356   | 2.728  | 0.006   |
| Human         | FRAG                                          | −0.994 | 0.273   | −3.640 | 0.000   |
| Human         | AGFIELD                                       | 4.796  | 0.840   | 5.712  | <0.001  |
| Home Range    | ISO                                           | −3.709 | 0.933   | −3.975 | <0.001  |
| Weather       | TEMP                                          | 0.446  | 0.185   | 2.407  | 0.016   |
| Interaction 1 | DAYNIGHT:Night × JULIAN S1                    | −15.344| 1.421   | −10.800| <0.001  |
|               | DAYNIGHT:Night × JULIAN S2                    | 10.075 | 1.676   | 6.011  | <0.001  |
|               | DAYNIGHT:Night × JULIAN S3                    | −1.644 | 3.412   | −0.482 | 0.630   |
|               | DAYNIGHT:Night × JULIAN S4                    | 5.112  | 2.113   | 2.419  | 0.016   |
| Interaction 2 | FRAG × DAYNIGHT:Night × Sex:Male              | 0.961  | 0.463   | 2.075  | 0.038   |
|               | FRAG × Sex:Male                               | 0.100  | 0.384   | 0.261  | 0.794   |
|               | FRAG × DAYNIGHT:Night                         | 0.408  | 0.328   | 1.244  | 0.214   |
|               | DAYNIGHT:Night × Sex:Male                     | 10.207 | 0.734   | 13.915 | <0.001  |
| Interaction 3 | TEMP × JULIAN S1                              | −0.549 | 0.269   | −2.037 | 0.042   |
|               | TEMP × JULIAN S2                              | 0.431  | 0.230   | 1.877  | 0.061   |
|               | TEMP × JULIAN S3                              | −1.835 | 0.486   | −3.774 | <0.001  |
|               | TEMP × JULIAN S4                              | −1.800 | 0.531   | −3.446 | <0.001  |

† Explanations for abbreviations are in Table 1.
‡ “S” stands for spline. Splines with five degrees of freedom were used to model the effect of JULIAN, which requires estimating four regression coefficients. We report the individual coefficients as S1–S4.
after accounting for movement rate (MOVEHR) and Julian date (JULIAN), may be due to a drop in activity (ACT) during daytime ($n = 5$, $\beta = -0.042$, SE = 0.010, $p < 0.001$) in fragmented areas. Activity levels for male bears ($n = 2$) did not show a significant relationship with our indices for habitat fragmentation ($\beta = -0.019$, SE = 0.017, $p = 0.258$).

We found evidence that bears moved more quickly when at the periphery of their home ranges (ISO) during spring and fall ($\beta = 0.297$, 0.429, SE = 0.136, 0.135, $p = 0.029$, 0.001 for spring and fall, respectively) relative to movements near the home range center. Conversely, when near the center of their home ranges, they had significantly higher HR than would be expected given their movement rate (Table 2).

During spring, higher ambient temperatures...
were associated with faster movements ($\beta = 0.080, SE = 0.007, p \leq 0.001$) and higher than expected HR (Fig. 8B). In fall, HR was negatively associated with ambient daily temperatures (Fig. 8B) despite faster movement rates ($\beta = 0.088, SE = 0.006, p \leq 0.001$).

**Indirect effects on bear heart rates**

In all seasons, when bears crossed roads, their rate of movement increased ($\beta = 2.63, 1.40, 1.27, SE = 0.106, 0.080, 0.080, p \leq 0.001$ for spring, summer, fall, respectively) but HR did not change beyond what was expected given the increased movement.
The updated model estimates (Appendix), utilizing all 12 bear-years (2009–2013), were similar to the original estimates (Table 2).

Road crossings were again the strongest positive influence on bear movement rates in all seasons (six of seven individuals) but road crossings were not common for these individuals (1.9% of movement steps). During spring and summer all three moved significantly faster near the periphery of their home ranges (ISO) than in the center, but only one bear displayed significantly faster movement rates during fall. During summer, two of the three bears moved through agricultural fields regularly (\( \bar{X} = 15.1\% \) of movement steps potentially included an agricultural crossing) and they displayed a pattern of increased rates of movement (although not significantly) in these fields. In the fall, all three bears significantly increased movement when located in agricultural fields and two bears which used crop fields (60.6% and 40.0% of fall locations) had significantly reduced movement rates when located in these fields.

**DISCUSSION**

The addition of HR monitoring to already common methods of movement monitoring provided novel insights into a bear’s view of its world. As black bear populations continue to expand into agricultural and other human-dominated landscapes, it is important to understand not only how, but why bears react in certain ways, and also appreciate that not all bears react the same. Our ability to simultaneously capture bears’ physiological status in conjunction with their locations has enabled us to control for movement when interpreting HR. We identified direct physiological responses to crop conditions.
fields and other anthropogenic landscape features, ambient temperature, and location of the bear within its home range, beyond the effects of their influences on movement.

**Temporal effects**

American black bears are known to alter their activity and movements among seasons (Amstrup and Beecham 1976, Garshelis and Pelton 1981, Garshelis et al. 1983, Bridges et al. 2004, Noyce and Garshelis 2010). We also observed seasonal changes in daily activity rhythms, but the patterns we observed were different than previously reported. Most previous studies of bears, especially American black bears, showed that they are most active during the day (summarized by Paisley and Garshelis 2006). It was previously reported that black bears usually only deviate from this pattern in fall, when they increase their level of nocturnal activity (Garshelis and Pelton 1980, Bridges et al. 2004). We observed, when looking at movements, that bears in northwestern Minnesota were also more nocturnally active in spring. We also observed large seasonal changes in HR, indicative of metabolic changes (Green 2011). However, the bears exhibited a temporal misalignment between HR and movement during the fall: metabolism decreased earlier and more rapidly than their movements. This may explain how bears are able to rapidly accumulate fat during hyperphagia (Hilderbrand et al. 1999). They feed on calorically rich food (Brody and Pelton 1988, Ditmer 2014), reduce activity during the day to avoid overheating, and slow their metabolism while not sacrificing rate of food intake, all to maximize weight gain. This strategy fits with Florant and Healy’s (2012) general hibernation model, which suggests a temporal lag between reductions in metabolic rate and food consumption to maximize fat accumulation.

**Human disturbance effects**

Agricultural fields and crops had dramatic effects on bear behavior. We anticipated that as bears quickly traversed agricultural fields, their HR would increase not only commensurate with their hastened movement, but also due to the stresses of being in an open environment with potential exposure to humans. In fact, bear HR’s were higher than would be predicted by movement rate alone, which we consider indicative of an acute stress response. Bears of both sexes were not commonly found in these areas, but due to the pervasiveness of agricultural land, they were forced to traverse them routinely. Metabolic costs increase for bears with the need to move greater distances between patches of habitat (Ellis et al. 2011) than within areas of natural habitat. In our study, female bears moved faster during the summer in agricultural areas relative to other land cover types, indicating that there is also an indirect cost associated with home ranges that incorporate more agricultural areas. We found that weekly home range size in this area was positively linked with the percentage of agricultural lands (Ditmer 2014), yielding the largest reported annual home ranges for the species (Ditmer 2014).

Whereas traversing agricultural fields where they did not forage increased energy expenditure for bears, the edible crops available in some fields provided tremendous energy gain for those bears that took advantage of this food source. Bears that fed on corn, oats, or sunflowers had slower movement rates, access to abundant calories, and several individuals had lower than expected HRs. Unlike foraging in natural areas, where intense foraging activity could cause HR to increase above what is expected given movement (movement is likely to be slow when foraging), bears saved energy by feeding on densely packed crops, and their HR showed no indication of being on alert. We observed (Ditmer 2014) that the benefits of these crops seem to be accrued disproportionately by large males and females without cubs, suggesting that some bears were being socially excluded from crop fields or exhibiting risk-aversion by staying away (e.g., females with cubs and juvenile bears). Bear foraging in corn and other crops has been well documented throughout North America (Landers et al. 1979, Elowe and Dodge 1989, Mattson 1990, Maddrey and Pelton 1995); our findings demonstrate that bears not only have access to plentiful calories, but that they are able to forage more easily and do not seem to incur acute stress while doing so. The highly predictable availability of edible crops also likely reduces chronic stresses associated with periods of reduced natural foods (Hellgren et al. 1993).

Many species show indications of elevated
stressed in fragmented habitats (MacArthur et al. 1979, Newcomb et al. 2003, Johnstone et al. 2012). However, Wasser et al. (2004) reported lower levels of cortisol, a stress-related hormone, in bears living in areas with high levels of human activity. Bourbonnais et al. (2013) found higher stress levels in male bears in areas with higher human disturbance, but found the opposite to be true in females. Our results were also mixed: whereas bears exhibited heightened HRs in agricultural areas, females had slower HRs during the daytime hours in areas with high habitat fragmentation. One explanation is that the reduced HRs exhibited by females were a result of reduced activity in response to human activities. Bears have been observed to limit diurnal foraging activity to avoid competitors (Schwartz et al. 2010) or in response to human presence (Ayres et al. 1986, Baruch-Mordo et al. 2014). Alternatively, what we observed may have been complicated by road crossing. The extensive road network in our study area created small habitat patches with high ratios of edge to habitat, thus creating high levels of FRAG (Spellerberg 1998, Trombulak and Frissell 2000). Roads are often associated with higher rates of movement (Coffin 2007, Dussault et al. 2007), just as we found. Female bears may view roads as “barriers of fear” (Eftestøl et al. 2014); they approached and crossed quickly, then slowed down after reaching a safe distance.

Home range effects

The periphery of an animal’s home range is typically in flux, changing position from one year to the next (Powell 2000). We expected HR to increase at the edges of the bear’s home range, where they would presumably feel less comfortable, and encounter other bears more often. Instead, bears located at the periphery of their home ranges exhibited high rates of movement but lower than expected HRs. We interpret this novel finding to suggest that movements at the home range periphery were more exploratory in nature (travel interspersed with some foraging), due to less familiarity with resources and possibly less preferred habitat. In contrast, bears in the core of a home range were likely focused on foraging in areas with better-known resources; foraging activity increases HR above what is predicted from the bears’ slow rate of movement.

Accordingly, Samson and Huot (1998) found that the core of female black bear home ranges in Ontario, Canada, contained better producing food resources than the periphery.

Weather effects

Temperature had a direct influence on HR, but the most notable effects occurred only early and late in the year. Previously, Toien et al. (2011) reported that bears returned to normal body temperatures after den emergence, but they maintained reduced metabolic rates for up to an additional three weeks. Our results show that after den emergence, bears exhibited higher HR on days with higher ambient temperature. We hypothesize that this relationship was related to phenology of early season vegetation; as temperatures in early spring increased, more green vegetation became available for consumption and this in turn promoted foraging, resulting in increased metabolism. During the fall, the relationship was reversed; HR decreased with rising temperatures. While preparing for hibernation, bears may increase weight by 50–100%, largely in the form of fat, and also grow a dense coat of underfur. In an effort to conserve energy and prevent overheating, they reduce activity during periods of warm temperatures and appear to become lethargic. Craighead and Craighead (1972) first described this pre-hibernation lethargic state, and noted that grizzly bears (U. arctos) exhibited higher levels of activity on cooler fall days.

Improvements and future research

The use of biologger technology in the fields of ecology and conservation biology is rapidly expanding and being applied in a wide variety of species to better understand the physiological responses of animals to their environment (Ropert-Coudert and Wilson 2005, Cooke et al. 2014). Whereas the devices that we employed enhanced our interpretation of American black bear behavior, they were not without some noteworthy limitations. For example, the monitors we utilized must be implanted and only stored two average HR values for each 24 hour period (daytime and nighttime), with eight hours not measured. Thus, we could not match fine-scale (sometimes hourly) locations from the GPS units with corresponding HR. Instead, we relied
on a sophisticated modeling approach that compared a bear’s suite of activities during the course of one 8-hour daytime and a 4-hour nighttime interval each day with its average HR for that interval. It should be noted, that we are currently employing and developing methodologies to utilize biologgers that record HR at much shorter intervals to overcome this limitation. Second, about half the implanted HR devices were rejected (expelled from their subcutaneous placements) by these bears, so our sample was reduced accordingly (Echols et al. 2004, Laske et al. 2005, Iaizzo et al. 2012). Despite a small sample size, however, we were encouraged that three post hoc datasets supported our model results. Large physiological datasets from a few individuals tend to contain highly autocorrelated data and must be analyzed and interpreted cautiously (Fieberg and Ditmer 2012). We expect that as biologger technology becomes more widely used, comparative and collaborative research efforts will provide even more reliable inferences and insights.

Developing a deeper understanding of the ecology and biology of species living in human-dominated landscapes is becoming increasingly important because of the expanding human footprint and reoccupation of native species to these geographies. Anthropogenic features on the landscape increased both the metabolic costs and the caloric rewards for a population of bears in northwestern Minnesota. The novel uses of biologger technologies will open new doors in ecology and biology by enabling physiological research to move from the lab to the field, and thus from the conceptual to the quantifiable. Future research should also increase collaboration with the medical community to incorporate and utilize the latest remote technology to capture meaningful physiological changes in free-roaming organisms at fine temporal and spatial scales.

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Table A1. Updated parameter estimates, standard errors, \( t \) statistics and \( p \) values for the covariates included in the top linear mixed (population) model assessing factors influencing heart rate in beats per minute for American black bears in northwestern Minnesota, excluding time spent in the den (2009–2013).

| Type                  | Covariates†‡ | \( \beta \) | SE(\( \beta \)) | \( t \)  | \( p \)   |
|-----------------------|--------------|-------------|----------------|--------|----------|
| Intercept             | None         | 37.560      | 3.575          | 10.507 | <0.001   |
| Movement              | MOVEHR       | 2.291       | 0.519          | 4.410  | <0.001   |
| Individual            | SEX: Male    | -10.484     | 2.921          | -3.590 | 0.005    |
| Temporal              | JULIAN S1    | 73.919      | 7.417          | 9.966  | <0.001   |
|                       | JULIAN S2    | 9.454       | 6.070          | 1.557  | 0.120    |
|                       | JULIAN S3    | 61.209      | 12.524         | 4.887  | <0.001   |
|                       | JULIAN S4    | 3.291       | 5.453          | 0.604  | 0.546    |
|                       | DAYNIGHT:Night | -1.089   | 1.250          | -0.871 | 0.384    |
| Human                 | FRAG         | -1.025      | 0.242          | -4.241 | <0.001   |
| Human                 | AGFIELD      | 5.822       | 0.812          | 7.168  | <0.001   |
| Home Range            | ISO          | -3.369      | 0.847          | -3.978 | <0.001   |
| Weather               | TEMP         | 0.517       | 0.167          | 3.091  | 0.002    |
| Interaction 1         | DAYNIGHT:Night × JULIAN S1 | -16.368 | 1.289 | -12.694 | <0.001 |
|                       | DAYNIGHT:Night × JULIAN S2 | 13.786 | 1.478 | 9.327   | <0.001 |
|                       | DAYNIGHT:Night × JULIAN S3 | 6.468 | 3.184 | 2.031   | 0.042  |
|                       | DAYNIGHT:Night × JULIAN S4 | 2.333 | 2.244 | 0.995   | 0.320  |
| Interaction 2         | FRAG × DAYNIGHT:Night × Sex:Male | 0.211 | 0.421 | 0.501   | 0.617  |
|                       | FRAG × Sex:Male | 0.037 | 0.371 | 0.098   | 0.922  |
|                       | FRAG × DAYNIGHT:Night | 1.132 | 0.260 | 4.359   | <0.001 |
|                       | DAYNIGHT:Night × Sex:Male | 13.059 | 0.668 | 19.547  | <0.001 |
| Interaction 3         | TEMP × JULIAN S1 | -1.228 | 0.226 | -5.446  | <0.001 |
|                       | TEMP × JULIAN S2 | 0.339 | 0.191 | 1.774   | 0.076  |
|                       | TEMP × JULIAN S3 | -1.531 | 0.442 | -3.467  | 0.001  |
|                       | TEMP × JULIAN S4 | -1.827 | 0.254 | -7.191  | <0.001 |

† Explanations for abbreviations can be found in Table 1.
‡ “S” stands for spline. Splines with five degrees of freedom were used to model the effect of JULIAN, which requires estimating four regression coefficients. We report the individual coefficients as S1–S4.