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Activity pattern plasticity may serve as an evolutionary adaptation to optimize fitness in an inconstant environment, however, quantifying patterns and demonstrating variation can be problematic. For American black bears *Ursus americanus*, wariness and habitat inaccessibility further complicate quantification. Radio telemetry has been the primary technique used to examine activity, however, interpretation error and limitation on numbers of animals available to monitor prevent extrapolation to unmarked or untransmittered members of the population. We used remote cameras to quantify black bear activity patterns and examined differences by season, sex and reproductive class in the Alleghany Mountains of western Virginia, USA. We used 1,533 pictures of black bears taken during 1998-2002 for our analyses. Black bears generally were diurnal in summer and nocturnal in autumn with a vespertine activity peak during both seasons. Bear-hound training seasons occurred during September and may offer explanation for the observed shift towards nocturnal behaviour. We found no substantial differences in activity patterns between sex and reproductive classes. Use of remote cameras allowed us to efficiently sample larger numbers of individual animals and likely offered a better approximation of population-level activity patterns than individual-level, telemetry-based methodologies.

Key words: activity patterns, American black bear, dogs, optimality theory, remote camera, Ursus americanus, Virginia

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Optimality theory suggests that animals maximize fitness by making decisions that balance resource access against physiological costs and risk of predation (MacArthur & Pianka 1966, Schoener 1971, Alexander 1996). Animals actively in search of resources or mates incur physiological costs and may be exposed to predation, and thus activity patterns should conform to this theory. However, quantification of activity patterns in natural settings has been constrained by methodological limitations (Halle & Stenseth 2000). Because of variation among individuals (Wagner, Hightower & Pace 2001), individual-level methodologies such as radio telemetry are limited in their inference to the response of transmittered individuals to environmental stimuli.

Investigations into black bear *Ursus americanus* activity patterns have relied on radio telemetry and based analyses on fluctuation in signal strength (Amstrup & Beecham 1976, Lindzey & Meslow 1977, Ayres, Chow & Graber 1986), distance between consecutive triangulations (Alt, Alt & Lindzey 1976), and motion-sensitive transmitters (Garshelis & Pelton 1980, Ayres et al. 1986, Larivière, Hout & Samson 1994, Wagner et al. 2001). Signal strength fluctuations can be misinterpreted due to signal interference, temperature fluctuations and slight animal movements, while triangulation requires multiple, accurate locations in a relatively short time frame or simultaneous readings from two stations (Lindzey & Meslow 1977, Garshelis & Pelton 1980, Garshelis, Quigley & Villarrubia 1982). Use of motion-sensitive transmitters is limited by the number of individual animals that can be transmittered and monitored throughout the entire diel period (Wagner et al. 2001). Intensive calibration with captive animals (Janis, Clark & Johnson 1999) can reduce interpretation error, however, discrimination between sedentary movements (such as lifting of the head while lying or sitting) and ambulatory activity may result in misclassification errors (Wagner et al. 2001). Whereas both sedentary movements and ambulatory activities are interesting from an ethological standpoint, optimization of ambulatory activity and associated access to resources and risk of predation has more bearing on fitness.

Simple automated photography systems have been used to measure small mammal activity since the late 1950s (Dodge & Snyder 1960, Osterberg 1962, Buckner 1964, Carthew & Slater 1991). In recent years, high-quality commercially constructed systems have become available (Kucera & Barrett 1993, Kucera & Barrett 1995) and are being used for a variety of wildlife research applications (Cutler & Swann 1999). Automated cameras have been used to estimate bear density (Mace, Minta, Manley & Aune 1994, Bowman, Chamberlain, Leopold & Jacobson 1996, Martorello, Eason & Pelton 2001) and to evaluate activity patterns for a variety of small mammal species (Cutler & Swann 1999). However, only recently have researchers used remote cameras to examine bear behaviour (Bridges, Fox, Olfenbuttel & Vaughan 2004). In reviewing possible applications of remote cameras to bear research, Garshelis, Coy & Kontio (1993: 315) concluded that documenting bear activity with cameras 'compared favourably' with telemetry-based techniques. Thus, our objectives were to 1) quantify and compare seasonal activity patterns, 2) determine whether activity patterns varied by sex and/or reproductive status, and 3) evaluate effectiveness of infrared-triggered cameras at bait stations to quantify activity.

Material and methods

Study area

Our study was conducted in Rockingham County on the George Washington and Jefferson National Forests in the Alleghany Mountains of western Virginia, USA. Elevations ranged within 480-1,360 m (Kozak 1970) and forest cover types included: eastern hemlock *Tsuga canadensis*, sugar maple-beech-yellow birch *Acer saccharum*, *Fagus grandifolia*, *Betula allegheniensis*, chestnut oak *Quercus prinus*, pitch pine *Pinus rigida*, white oak-black oak-northern red oak *Q. alba*, *Q. velutina*, *Q. rubra*, northern red oak, yellow poplar-white oak-northern red oak *Liriodendron tulipfera*, eastern white pine *P. strobus*, mountain laurel *Kalmia latifolia* and scrub oak *Q. ilicifolia* (Rawinski, Fleming & Judge 1994). Bear-hound training seasons, during which bears could be chased and treed with hounds but not hunted, were held in September. Bear-hound training was allowed only during daylight hours.

Data were gathered in late summer (1998-2002) and early autumn (1998-2001) in conjunction with data gathered for mark-resight population estimation. Marking and subsequent identification of individual bears was necessary to evaluate effects of sex, age or reproductive status on activity patterns. We captured bears with Aldrich spring-loaded foot snares and culvert traps from late May through early August (Johnson & Pelton 1980), sedated them with a mixture of ketamine hydrochloride and xylazine hydrochloride (200:100 mg/ml; 1 ml/45 kg), fitted them with colour-coded, individual-specific streamers attached to coloured ear tags (Martorello et al. 2001), and, in some cases, equipped them with radio transmitters (ear tags or collars). Streamers were replaced on bears recaptured in subsequent summers. Additionally, we weighed and measured each bear, determined gender and reproductive status, and removed a tooth for aging (Willey 1974, Carrel 1994, Keay 1995). The Virginia Polytechnic Institute and State University Animal Care and Use Committee approved all animal handling protocols.

Camera surveys

We constructed 50 camera sites near the center of alternating 1-km^2 cells on a 100-km^2 grid. Not all sites contained an infrared-triggered camera at every sampling

Figure 1. A marked and ear tag-transmittered (right ear) American black bear visiting a camera site in the Alleghany Mountains of Virginia, USA on the morning of 3 August, 2002. Note the time and date stamp in the lower left corner of the photograph.

interval due to budgetary constraints and destruction of cameras by bears after deployment. The number of sites with infrared-triggered cameras ranged from 11 in October 1998 to 49 in August 2002.

We conducted two camera surveys each year with each survey lasting approximately two weeks. Summer surveys were conducted between 29 July and 31 August and autumn surveys between 1 and 27 October. Data collection and baiting were not conducted during September due to presence of hounds and hunters. During 1998-2002, we used CamTrakker® (CamTrak South, Inc., Watkinsville, GA., USA) cameras with infrared triggers, multi-shot capability, adjustable delays between photographs and photographic stamps identifying the date and time each picture was taken (Fig. 1). In 2001, we added infrared-triggered DeerCam® (Non Typical, Inc., Park Falls, WI., USA) cameras. Like the CamTrakker, these cameras were multi-shot and provided time and date stamps. We set a 10-minute delay between photographs to allow multiple bears to be photographed in short periods of time while minimizing incidence of multiple shots of individual bears during one visitation. We used 24- or 36-exposure 400ASA film.

We nailed baits with fencing staples 2-3 m off the ground on large trees. We attached cameras to smaller trees with wire (CamTrakker) or drawstrings (DeerCam) and locked them in place with security cables. We positioned cameras parallel to and facing the bait 1-3 m off the ground (depending on slope). We placed baits 2-4 m from the cameras and aligned them from north to south (or vice versa) to avoid morning and evening glare. We checked cameras and rebaited every 2-4 days. Baits consisted of pastries placed in red mylar produce bags and soaked in molasses. We poured extra molasses on bait trees around the bait bag to act as a scent lure and allow for additional investigation and photograph opportunities of other bears after baits were consumed.

Analyses

We examined each picture to determine if the bear was marked and identifiable. Bears were considered identifiable if pictures clearly showed any attached transmitters, ear tags or streamers. We avoided counting multiple pictures of the same individual during one visitation by using a 60-minute rule in which multiple pictures taken within 60 minutes at the same site of the same identifiable bear, or of bears that we could not identify as different, were excluded from analyses. We determined sex and reproductive status based on individual identification via coloured streamers and on the presence of cubs in photographs. Females that were not nursing when handled during the summer or bears known to have had yearlings the previous winter were classified as females without cubs. Females were categorized as having cubs if they were observed with cubs earlier in the year, were lactating and showed evidence of nursing when captured during the summer, or were with cubs in photographs.

We divided each day into four periods. Morning and evening were defined as 240-minute periods including the 120 minutes before and after sunrise and sunset, respectively. Night was defined as ≥121 minutes after sunset until 121 minutes before sunrise, and day was ≥121 minutes after sunrise until 121 minutes before sunset.

We used all pictures conforming to the 60-minute rule to graphically represent overall activity patterns. We only used pictures of individuals that could be identified via their streamer combinations for compositional analyses of class-specific selection of activity time periods. Compositional analysis was designed to provide a measure of use versus availability for habitat selection studies (Aebischer, Robertson & Kenward 1993). However, it can be modified to examine activity patterns by substituting use with activity during a particular time period, and availability with proportion of a 24-hour day this time period comprises. We assumed independence of individual animals because bears generally are solitary, and we considered adult females with cubs to reflect only the choice of the adult female. Radio telemetry data analyzed by compositional analyses generally are characterized by relatively large numbers of locations (and accordingly, potentially large variation in sample size) on a relatively small number of individuals. Aebischer et al. (1993) recommended weighting log-ratios by number of locations only if variation in sample size was large. Because our data were characterized by relatively few observations (and relatively small variation in sample size) on a large number of individuals, we did not weight log-ratios based on the number of locations. When there were no observations for a particular time period we substituted values one order of magnitude smaller than the smallest observation for each individual animal (Aebischer et al. 1993). We pooled years because sample sizes were not sufficient for statistical comparisons among years.

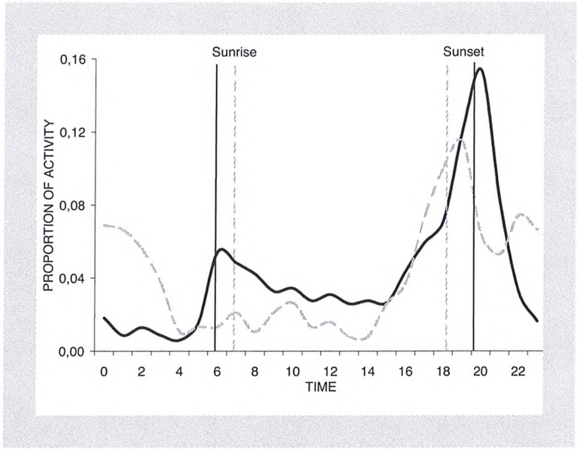

Figure 2. Daily activity patterns of black bears during summer (—) and autumn (- - -) based on 1,533 pictures taken with remote cameras in the Alleghany Mountains of western Virginia, USA, during 1998-2002. Summer and autumn include photographs taken during 29 July - 31 August and 1-27 October, respectively. Sunrise and sunset are based on 15 August for summer and 15 October for autumn. Proportion of activity is expressed by the total number of photographs that were taken during each hour, and time is U.S. eastern standard time.

Results

During 1998-2002, we marked 211 individuals (117 males (M) and 94 females (F)) with streamers and identified 135 (71M, 64F) of these bears in our camera

Table 1. Compositional analyses of activity period rankings for black bears based on photographs taken with remote cameras in the Alleghany Mountains of Virginia, USA during 1998-2002. Summer patterns were based on 571 pictures of 123 (64M, 59F) bears taken between 29 July and 31 August, 1998-2002, and autumn patterns were based on 142 pictures of 53 (20M, 33F) bears taken between 1 and 27 October, 1998-2001. Activity patterns were non-random (P < 0.001) for all six season and sex-class combinations. Significance levels based on t tests (Aebischer et al. 1993) of P < 0.01, P < 0.1, and P > 0.1 between two consecutively ranked time classes are indicated by >>>, >> and >, respectively.

Season	Sex	Time period rankings						
Summer	♂♂	Evening	>>>	Day	>	Night	>	Morning
	♀♀	Evening	>>>	Day	>>>	Morning	>	Night
	Combined	Evening	>>>	Day	>>>	Morning	>	Night
Autumn	♂♂	Night	>	Evening	>>	Morning	>	Day
	♀♀	Night	>	Evening	>>>	Day	>	Morning
	Combined	Night	>>	Evening	>>>	Day	>	Morning

surveys. We used 571 pictures of 123 (64M, 59F) individuals in summer and 142 pictures of 53 (20M, 33F) individuals in autumn for compositional analyses. We used 1,533 pictures of bears to graphically display activity patterns (Fig. 2).

Graphical representation of bear activity patterns in summer revealed a small peak in the morning, followed by sustained, moderate levels of activity throughout the day, and punctuated by a spike in activity during the hours immediately preceding and following sunset (see Fig. 2). Little activity was recorded at night. Compositional analyses of data confirmed that evening followed by day were the periods of highest bear activity in summer, however, the morning peak visible in Figure 2 was not statistically significant (Table 1).

In autumn, we observed a similar, though smaller, activity peak in the evening (see Fig. 2). However, sustained levels of nocturnal activity replaced the sustained diurnal activity exhibited in summer and no morning peak was evident. Results from compositional analyses further demonstrated greater night and evening versus morning and daytime activity of bears (see Table 1).

Compositional analyses revealed no substantial difference in activity pattern between male and female bears (see Table 1). Females with cubs and females without cubs exhibited the same activity pattern during the summer. Due to limited sample size, we could not compare females with cubs and females without cubs in autumn.

Discussion

We found that bears in our study area exhibited a generally vespertine activity pattern in both summer and autumn (see Fig. 2). An evening activity peak was also documented in denning black bears in Virginia (Bridges et al. 2004). Crepuscular activity peaks were reported for black bears in California (Ayres et al. 1986), Idaho (Amstrup & Beecham 1976), Tennessee (Garshelis & Pelton 1980) and Washington (Lindzey & Meslow 1977), but none reported substantially different levels of morning versus evening activity. Furthermore, our results differ from those reporting that black bears are primarily diurnal (Larivière et al. 1994) or nocturnal (Rogers 1970). In the only published reference to the use of cameras for quantifying bear activity patterns, Garshelis et al. (1993) report, but do not elaborate upon, a single graph of summer activity patterns in Minnesota taken from Swanson (1990) that shows a pattern similar to results from our summer surveys.

Proportional increase in nocturnal activity in autumn was demonstrated in Tennessee (Garshelis & Pelton 1980) and Idaho (Amstrup & Beecham 1976). On our study area, however, not only did proportional nocturnal activity increase, but bears became more nocturnal than diurnal. Black bears (Ayres et al. 1986, Beecham & Rohlman 1994) and other secretive species, such as mountain lions *Puma concolor* (Van Dyke, Brocke, Shaw, Ackerman, Hemker & Lindzey 1986), may become more nocturnal with increasing human disturbance.

In Virginia, chasing bears with hounds is a longstanding tradition. The effects of hunting with hounds on bear harvest (Litvaitis & Kane 1994), condition (Massopust & Anderson 1984), and home-range (Higgins 1997) have been evaluated. Possible effects of hounds on bear behaviour have not been examined. Rockingham County consistently experiences among the highest bear harvest and hunter activity levels in Virginia (Martin & Steffen 2000), and the September bear-hound training season that took place between our summer and autumn surveys may have influenced bear activity patterns. Hunters training their hounds generally began at sunrise, involved 7-12 hounds per chase, with chases often lasting into the afternoon (Higgins 1997). Although evidence is correlative, the relatively high sunrise-afternoon activity exhibited prior to the hound training season replaced by nocturnal activity directly following the hound training season is consistent with optimization theory if the benefits of diurnal activity are outweighed by the costs of being chased by hounds. However, no negative effects on bear condition and survival have been associated with hounds (Massopust & Anderson 1984, Higgins 1997), and the similar, albeit less dramatic, increase in nocturnal activity documented in unhunted populations (Amstrup & Beecham 1976, Garshelis & Pelton 1980) indicate other unknown factors likely contribute to autumnal nocturnality.

Similar to Larivière et al. (1994) in Quebec, Canada, and Lindzey & Meslow (1977) in Washington, we found that bears with and without cubs exhibited similar activity patterns in summer. These results differ from those of Ayres et al. (1986) in California and Garshelis & Pelton (1980) in Tennessee, who found that the presence of cubs modified activity patterns. Although differences in natural food availability (e.g. summer soft mast versus autumn hard mast) confound interpretation, the reduced visitation rates we documented at camera sites during autumn were consistent with the findings of Garshelis & Pelton (1980), who observed less overall activity in autumn than in the summer.

A concern with camera-based assessment is whether the presence of bait might modify bear behaviour. We do not believe this confounded results in our study because our 2-week sampling periods offered little time for habituation to bait sites, and because 64.5% of the 1,419 photographs where presence/absence of bait could be determined occurred after bait had been removed during a previous visitation, indicating bait in combination with molasses acted effectively as a scent lure and the absence of bait did not preclude other bears from visiting the site. Additionally, bears likely acquire knowledge of natural food sources prior to visiting them, yet they still must decide at what times foraging optimizes fitness. We believe our bait sites did not modify bear activity, and that they visited them as they would other natural food sources.

Our camera setup technique was similar to those deployed in previous population estimation studies (Mace et al. 1994, Bowman et al. 1996, Martorello et al. 2001). We found that a 10-minute delay between photographs was sufficient to document multiple bears visiting the same site during times of high activity while not expending excess film on multiple pictures of the same bear during a single visitation. If cameras are used to document activity patterns in an unmarked population, researchers might extend this delay to ≥1 hour because bears generally lack naturally occurring and easily identifiable marking patterns; thus individuals cannot be reliably identified, and independence cannot be verified without an artificial marking system.

We found that placing baits on trees with a large diameter at breast height (i.e. > 40 cm; Martorello et al. 2001) and leaning away from the camera increased our efficiency in identifying streamer combinations on individuals by helping to assure the camera system was triggered when the bear climbed with its back (and accordingly its streamers) towards the camera. Placement of cameras 2-3 m from the bait trees provided the best distance for streamer and thereby individual bear identification while allowing sufficient flexibility in camera and motion sensor alignment. Cameras placed >1 m from the ground were disturbed less frequently than those placed at the bears' eye level. Use of a large, numbered sign stapled just above the bait provided a permanent record of plot location. Additionally, these signs allowed us to briefly describe the purpose of the cameras and provide contact information in an effort to prevent tampering or theft by any humans discovering the site. We recommend using light brown (or other earth tone) signs to avoid advertising the presence of equipment to human passersby. Finally, checking and rebaiting the camera sites at ≤ 3-day intervals allowed us to realign or replace cameras that were disturbed or damaged by bears.

We found that remote cameras offer a potentially valuable method for quantifying bear activity. Remote cameras are advantageous because they 1) require less intensive monitoring when compared with telemetry-based assessment, 2) can be used in conjunction with mark-resight studies, 3) sample untransmittered and unmarked individuals and, thus, a greater proportion of the population, and 4) can be conducted without capturing and handling bears. Although handling animals allowed for more in-depth statistical analyses and examination of covariates, biologists interested in examining general activity patterns could potentially deploy cameras and obtain coarse approximations without capturing any individuals.

In general, we concur with Garshelis et al. (1993) that camera-based activity assessments offer advantages over telemetry-based assessments. However, telemetry-based studies may offer better individual-level precision when the habits of specific classes of animals (e.g. females with and without cubs, nuisance bears) are the primary focus. Researchers should carefully consider study objectives prior to selecting a method.

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