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Original article

Behavioural response of moose *Alces alces* and brown bears *Ursus arctos* to direct helicopter approach by researchers

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Helicopters are used for numerous wildlife management and research purposes, but can alter wildlife behaviour and influence baseline data collection. We investigated reactions of GPS-collared moose *Alces alces* and brown bears *Ursus arctos* to short-term helicopter approaches by researchers. Moose responded with up to 10 times greater movement rates for up to two hours following a helicopter approach and moved into more rugged terrain. Brown bears decreased their speed and remained within similar habitat types and terrain. The movements were influenced only about two hours and did not influence the size of the activity areas. Contrary to our predictions, brown bears responded with a somewhat calmer response than moose, illustrating response differences in large herbivores and carnivores. This difference in response might be because brown bears are actually less disturbed than moose by direct helicopter approaches or because of a difference in tactical behaviour between brown bears and moose following disturbance. Researchers and managers should thus be cautious in using knowledge from one species to predict or perceive disturbance response in another species or taxa.

Key words: aircraft, Alces alces, brown bears, disturbance, GPS, moose, overflight, Sweden, Ursus arctos

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Aircraft are frequently used in wildlife management and research projects on large mammals because of the increased efficiency in data collection in the field. Large mammals in general have large home ranges and can be readily observed from low-flying aircraft (Jachmann 2002). Study populations of large mammals are also often found in remote areas, which makes helicopters a cost-efficient method and sometimes the only method available for locating and observing large mammals. For these reasons, helicopters are frequently used in capture and radio-marking (Arnemo et al. 2006) and for monitoring and population estimation (Jachmann 2002, Linklater & Cameron 2002) of large mammals. Although the potential for aircraft to alter wildlife behaviour has been appreciated for many years (see Bleich et al. 1990 for review), direct approaches by researchers are used as a method for observing large mam-

mals that already have been radio-marked (Solberg et al. 2006).

An approaching and low-flying aircraft may affect the behaviour and ecology of wildlife. A range of species from birds to terrestrial and marine mammals react negatively to aircraft surveys and over-flights by e.g. increasing their movements and vigilant behaviour, decreasing foraging efficiency by shifting habitat and altering grouping patterns (Delaney et al. 1999, Linklater & Cameron 2002, Patenaude et al. 2002, Frid 2003, Southwell 2005, Tracey & Fleming 2007). Under certain conditions animals can become habituated to the disturbance (Miller & Gunn 1980, Stockwell et al.1991, Hughes et al. 2008) but the disturbance effects normally increase with increasing intensity of the harassment (Bayne et al. 2000, Goldstein et al. 2005). The proximity and the direction of the aircraft in relation to the animals influence the effect of the disturbance, with more severe reactions by the animals to direct approaches and short distances to the aircraft (Stockwell et al. 1991, Frid 2003).

The justification for disturbing animals in conservation, research and management projects is sometimes questioned, thus, for both ethical and scientific reasons, researchers should focus on animal welfare and know the effects of the necessary disturbances on the study animals and research results. Both short-term and long-term negative effects of capture on animal welfare have been documented in large mammals (Alibhai et al. 2001, Côté et al. 1998, Cattet et al. 2008). However, there has been little attention on the disturbance effects of helicopter approaches in research projects (Scotton & Pletscher 1998). The effects of helicopter disturbance on large mammals have been documented for ungulates, mostly from observing the animals during over-flights by helicopters in recreational or exploration traffic (Stockwell et al.1991, Côté 1996) and during aerial surveys (Bleich et al. 1990, 1994, Linklater & Cameron 2002). The experimental overflights show that ungulates react more severely to threatening approaches (more direct approaches or at a shorter distance; Frid 2003, Goldstein et al. 2005, Tracey & Flemming 2007) but little is documented on the behaviour in large mammals in response to a helicopter directly approaching a single focal animal during research projects. The effects of direct helicopter approaches on large carnivores have not yet been reported even though routine helicopter approaches are used in many large carnivore projects.

To avoid biassed results in wildlife studies using helicopters, it is essential to know if, how and for how long an animal alters its normal behaviour following the potential disturbance. Such knowledge not only includes the impact of the disturbance stimuli themselves, but also a comparison of the animal's behaviour in undisturbed and potentially disturbing conditions. This becomes even more important with the current transition from low-intensity data collection using VHF radio-collars to the high-intensity GPS-based data collection used in studies of large mammals such as moose *Alces alces* and brown bears *Ursus arctos* (Moe et al. 2007, Dettki & Ericsson 2008). Until now all studies investigating helicopter disturbance have used data from direct observations or low-intensity relocations of VHF radio-collared animals.

In our study we investigated how GPS-collared moose and brown bears in Sweden reacted to helicopter approaches by researchers to count offspring, document survival or to find accompanying unmarked animals for capture. We investigated potential changes in movement patterns, activity area use, habitat use by individuals before and after the helicopter approaches and differences between the two species. In birds, Blumstein (2006) found that body size and age of first reproduction explained much of the variation in disturbance tolerance and that species that capture live prey or are highly social are relatively wary. The evolutionary origin of wariness is explained by 'carry-over effects' from selection for other traits, i.e. that predators should be more attentive to movements (Blumstein 2006). Following this reasoning, we predicted that the brown bear, a large carnivore, should be more flighty and, thus, more disturbed by helicopter approaches than the moose, a large ungulate. This should be expressed by longer movements during and after the disturbance stimuli, i.e. the helicopter approaches.

Material and methods

Our study was conducted in two areas in northern Scandinavia approximately 600 km apart. We studied moose in the counties of Västerbotten and Norrbotten in Sweden, and in Nordland, Norway (65°38' N,15°47' E; midpoint). The moose study area, which covers 23,000 km^2, is characterised by boreal and mountainous forest dominated by Scots pine *Pinus sylvestris*, Norway spruce *Picea abies*,

birch *Betula pubescens* and willow *Salix* sp. The area is sparsely populated by humans and has a low road density (220 m road/km^2). The average elevation is 1,073 ± 464 m a.s.l. and the mean temperatures in January and July are -13° C and 13° C, respectively. Snow cover lasts from the beginning of October until late May and the vegetation period is about 110-130 days (Helmfrid 1996).

We studied the bears in the counties of Dalarna and Gävleborg, south-central Sweden (61°25' N, 14°29' E). In the bear study area covering 4,363 km^2, the rolling landscape consists of intensively managed boreal forest dominated by Scots pine or Norway spruce mixed with deciduous trees in earlier successional stages with a median average habitat patch size of 22,500 m^2 (Moe et al. 2007). Although roads are common (929 m road/km^2), the area is sparsely populated by humans. The average elevation is 462 ± 170 m a.s.l., the average precipitation is 600-1,000 mm annually (Helmfrid 1996) and the mean temperatures in January and July are -7° C and 15° C, respectively. Snow cover lasts from late October/early November until early May and the vegetation period is about 150-180 days (Helmfrid 1996). Both moose and bears are intensively hunted in both study areas.

Moose and bears were immobilised and equipped with GPS Plus neck collars with GSM lateral modems (Vectronic Aerospace 2003; for details see Arnemo et al. 2006). The locations were recorded every hour for moose and every 30 minutes for bears and were sent as text messages containing packages of seven locations to a database server using the digital cell phone network (Dettki et al. 2004). All incoming locations were reviewed for their validity, with only three-dimensional locations being used in the analyses. Following common guidelines for precision, we only used locations with a dilution of precision (DOP) value ≤ 5 in our analyses (IOC 2006), which resulted in a location omission of 21.5%.

In the period 2003-2007, 46 adult female moose (3-11 years old) and 17 adult female bears (3-12 years old) were approached by researchers in a helicopter observing the animals to ascertain their reproductive success and survival, and some of the bears were approached to ascertain companionship with male bears for capture. Most individuals were disturbed more than once (with a maximum of seven times). Moose were approached both in winter (October-March) when the ground was covered with snow and in summer (April-September), whereas bears were only approached in the non-hibernating period (May-October). Approaches were omitted from the analysis when the focal animal or any accompanying animals were captured. The helicopter only approached within 50-100 m of the focal animal to allow visual observation and left as soon as the status was determined, which typically lasted < 1 minute. We noted the time during which the focal animal was observed from the helicopter.

We calculated the rate of movement (m/hour) of the focal animals in 1-hour intervals using GPS positions. Due to the occasional lack of GPS reception, the movement rate was calculated between two successive locations with a more than 1-hour difference in time, but with a maximum of 2-hour time difference. All movement rates were assigned to the time of the latter position in the time interval. We compared the rate of movement with the rate of movement the previous day during the same hour of the day using a paired t-test. We did this to control for potential effects of circadian changes in movement of the moose and bears. Due to the occasional lack of GPS reception, the sample sizes in our analysis varied. We compared the size of three different activity areas used by the animals before and after the approaches. The baseline area was defined as the minimum convex polygons (MCP) of the locations 27-50 hours prior to the approach, the pre-disturbance area was defined as the MCP of the locations 0-24 hours prior to the approach and the post-disturbance area was defined as the MCP of the locations 2-26 hours after the approach. We separated the locations used for the activity area calculations by two hours, excluding the first two hours of immediate disturbance (the flight response) between the pre-disturbance area and the post-disturbance area, and a similar time gap between the baseline area and the pre-disturbance area. We established the 2-hour time gap between the baseline area and the pre-disturbance area to counter bias in the calculations of overlap between the activity areas.

We extracted Swedish Land Cover data (SMD) which is a raster with 25 × 25 m pixels for each moose and bear location. We then reclassified the SMD categories and generated four categories for bear habitat data (1) deciduous forest, 2) coniferous forest, 3) open pasture and 4) open young forest and open land). Due to differences in forage aspects, we separated open young forest and open land for moose data, and thus generated five categories.

SMD data for moose in Norway were not available and so we excluded these from the moose analysis. We also aggregated the habitat categories by assigning categories 1 and 2 as closed habitat and categories 3-5 as open habitat. We did this to explore whether bears and moose shifted between closed and open habitat after being disturbed. We compared the topographic ruggedness index (TRI) for the locations in the pre-disturbance and post-disturbance areas. TRI is a measurement developed by Riley et al. (1999) to express the amount of elevational difference between adjacent cells of a digital elevation grid. The process essentially calculates the difference in elevation values between a centre cell and the eight cells immediately surrounding it.

Using a linear mixed model with repeated measures, we compared the frequency of use of the habitat categories among the three activity areas for each individual, as well as whether there was a shift in use of closed and open habitat. The different activity areas were assigned as fixed factors and the individuals as a random factor, nested within activity areas, due to replicated disturbances. Because the frequencies of use were not normally distributed, we transformed the data into ranks and used them in the linear mixed model. Covariance decreased with distance in time and, therefore, First-Order Autoregressive (AR(1)) appeared to be the most appropriate covariance model. To avoid inflation of type I error rates and, as recommended for repeated measures, we used the 'KENWARD-ROGER' (KR) correction (Littell et al. 2006). The Tukey Post-Hoc test was used to evaluate differences among activity areas.

We fitted linear mixed models for TRI as a response variable with the explanatory binomial variable 'before disturbance' (locations in the pre-disturbance area) = 0 and 'after disturbance' (locations in the post-disturbance area) = 1 and the individual moose or bear as a random variable using the lme function in R (the nlme library; R Development Core Team 2005). TRI were log transformed prior to analysis to comply with the requirement of normality of the response variable in the models. We used the statistical packages R 2.0.1 (R Development Core Team 2005) and SAS 9.1.3 (SAS Institute Inc., Cary, North Carolina, USA) in all statistical analyses and the software ArcGIS 9.2 (ESRI, Redlands, California, USA) in all GIS calculations. The significance level was set at $P < 0.05$.

Results

We approached the 46 female moose with helicopters for a total of 88 times and the 17 female bears for a total of 62 times. Most of the animals were moving

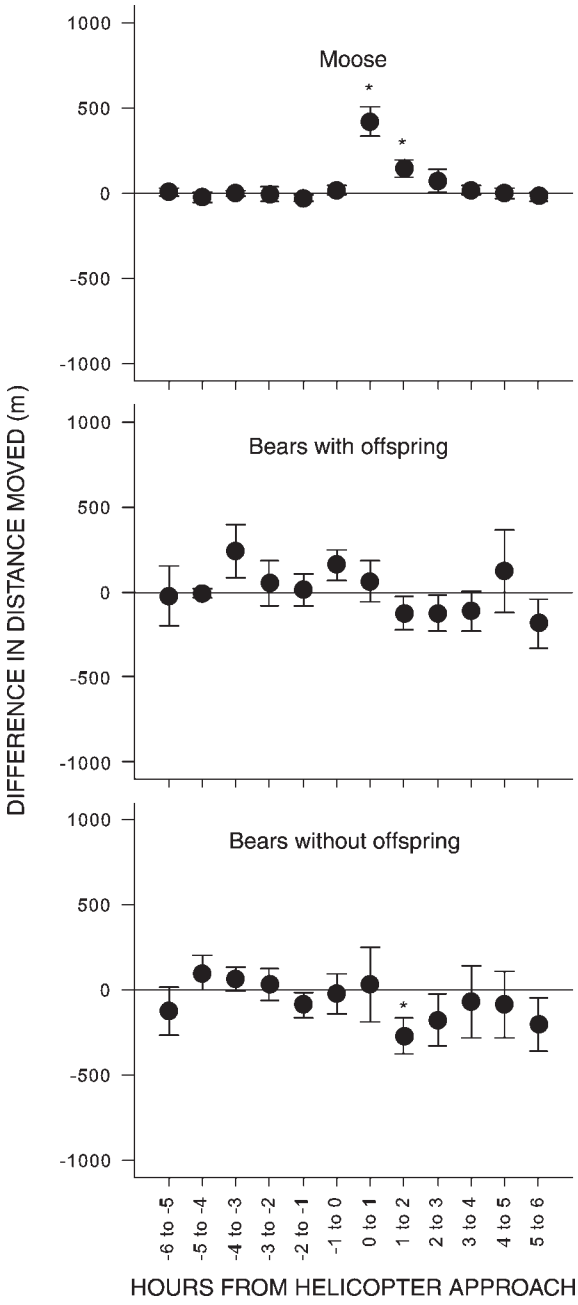

Figure 1. Difference in distance moved (m ± SE) in adult female moose and adult female brown bears with and without offspring during 1-hour periods before and after direct helicopter approach by researchers in Scandinavia compared with the same hour the previous day during 2003-2006. Statistically significant differences of the paired t-test are indicated with asterisks.

Table 1. Average speed (in m/hour ± SD) of adult female moose and adult female brown bears approached directly by researchers in helicopters in Scandinavia during 2003-2006 and results of paired t-tests of differences.

Species	Hours from helicopter approach	N	Average speed		t	df	P
				The same hour on the previous day			
Moose	6 to 5	53	53 (102)	49 (84)	0.223	52	0.824
	5 to 4	46	41 (83)	64 (204)	-0.717	45	0.477
	4 to 3	51	57 (92)	156 (512)	-1.442	50	0.155
	3 to 2	43	82 (221)	87 (226)	-0.103	42	0.919
	2 to 1	51	29 (68)	54 (99)	-1.588	50	0.119
	1 to 0	50	99 (181)	64 (92)	1.272	49	0.209
	0 to 1	41	467 (525)	46 (120)	4.873	40	0.000
	1 to 2	42	210 (296)	70 (169)	2.967	41	0.005
	2 to 3	51	180 (368)	105 (283)	1.137	50	0.261
	3 to 4	58	139 (251)	111 (257)	1.129	57	0.264
	4 to 5	68	91 (150)	86 (200)	0.165	67	0.870
	5 to 6	60	v77 (105)	89 (203)	-0.439	59	0.662
Bears with offspring	6 to 5	16	335 (449)	358 (487)	-0.128	15	0.900
	5 to 4	17	70 (101)	80 (111)	-0.374	16	0.714
	4 to 3	18	349 (668)	110 (235)	1.498	17	0.153
	3 to 2	17	181 (438)	131 (289)	0.374	16	0.713
	2 to 1	19	201 (311)	187 (358)	0.144	18	0.887
	1 to 0	15	232 (324)	73 (83)	1.769	14	0.099
	0 to 1	14	242 (343)	182 (260)	0.493	13	0.630
	1 to 2	14	185 (418)	310 (417)	-1.287	13	0.221
	2 to 3	12	40 (23)	165 (361)	-1.190	11	0.259
	3 to 4	14	255 (588)	369 (597)	-0.964	13	0.353
	4 to 5	13	441 (573)	321 (555)	0.491	12	0.632
	5 to 6	13	200 (238)	386 (482)	-1.295	12	0.220
Bears without offspring	6 to 5	39	310 (622)	435 (747)	-0.893	38	0.377
	5 to 4	35	549 (743)	448 (599)	0.998	34	0.325
	4 to 3	34	309 (539)	244 (417)	0.903	33	0.373
	3 to 2	32	377 (743)	343 (608)	0.362	31	0.720
	2 to 1	30	215 (405)	300 (600)	-1.148	29	0.260
	1 to 0	24	221 (376)	240 (478)	-0.161	23	0.873
	0 to 1	20	575 (646)	540 (702)	0.154	19	0.879
	1 to 2	23	229 (395)	496 (644)	-2.501	22	0.020
	2 to 3	32	284 (512)	457 (674)	-1.125	31	0.269
	3 to 4	25	459 (708)	526 (903)	-0.315	24	0.755
	4 to 5	19	681 (803)	764 (1114)	-0.434	18	0.670
	5 to 6	24	410 (669)	612 (864)	-1.318	23	0.200

Table 2. Generalised linear mixed models of the effects of being accompanied by offspring (Yes/No), season (summer or winter for moose) and number of times previously approached by helicopter on the log distance moved per hour during the first hour for 43 adult female moose approached 58 times, and during the second hour for 15 adult female bears approached 63 times by helicopters with researchers in Scandinavia during 2003-2006.

Species	Explanatory variable	β	SE	df	t	P
Moose (first hour)	Calves (Yes)	-0.0692	0.2080	12	-0.333	0.745
	Season (Summer)	-0.0828	0.2023	13	-0.409	0.689
	Number of approaches	0.1993	0.1706	14	1.169	0.262
Bears (second hour)	Number of approaches	0.0646	0.099	46	0.650	0.519
	Cubs (Yes)	-1.1122	0.491	47	-2.263	0.028

away from the helicopter when observed. The moose were approached at 12:00 ± 2 hours (mean ± SD) and the bears at 13:00 ± 6 hours. The average mean distance moved per hour in the 24-hour period prior to an approach was 70 ± 62 m (N = 83) for moose and 352 ± 284 m for bears (N = 62). We found no difference in the average mean distance that moose moved in the 24-hour period prior to summer and winter approaches (t = -1.00, df = 81, P = 0.32, N = 57 and N = 26, respectively) and there was no difference in the distance moved by 60 moose with calves and 19 without calves (t = -0.52, df = 77, P = 0.60). Bears with cubs (N = 21) moved less than bears without cubs (N = 40) in the 24-hour period prior to the approaches (on average 151 m/hour and 461 m/hour, respectively; t = -5.46, df = 59, P < 0.01).

During the first and the second hour after an approach, the moose moved on average 10 times and three times farther per hour, respectively, than during the same hour the previous day, but this effect disappeared after two hours (Fig. 1 and Table 1). Bears did not change movement patterns in the first hour after the approach but, contrary to moose, bears without offspring moved significantly less in the period 1-2 hours after the approach (see Fig. 1 and Table 1). The distance moved per hour by moose during the first hour after the helicopter approach was neither influenced by the number of times that the moose had been approached previously by helicopters, the season nor if the female was accompanied by a calf (Table 2). Bears were not influenced by the number of times they had been approached, but females accompanied by cubs moved less than females without cubs the second hour after the helicopter approach (see Table 2).

The average size of the area used during the periods 27-50 hours prior to (the baseline area), 0-24 hours prior to (the pre-disturbance area) and 2-27 hours after (the post-disturbance area) the helicopter approach was 27 ± 59 ha, 21 ± 42 ha and 23 ± 34 ha for moose (N = 77), 220 ± 396 ha, 302 ± 632 ha and 237 ± 393 ha for bears with offspring (N = 22) and 974 ± 1,129 ha, 853 ± 854 ha and 1,001 ± 929 ha for bears without offspring (N = 38), respectively. We found no significant difference in size among the activity areas for either species (Table 3). In 63% of the 83 cases for moose, the baseline areas overlapped with the pre-disturbance areas, whereas only 32% of the pre-disturbance areas overlapped with the post-disturbance areas. The proportion of overlap was 77 and 68% for 22 bears with offspring and 68 and 68% for 38 bears without offspring, respectively. For moose, the distance between the centres of the pre-disturbance area and the post-disturbance area was on average 1,237 m and 44% longer than the distance between the centres of the baseline area and the pre-disturbance area (Paired t-test: t = 2.2, df = 76, P = 0.034). For bears these distances were not significantly different and were on average 1,784 to 1,431 m (Paired t-test: t = 0.913, df = 21, P = 0.372) for bears with offspring and 3,537 to 3,917 m (Paired t-test: t = -0.819, df = 37, P = 0.418) for bears without offspring, respectively.

SMD data were available for 33 individual moose and 59 approach events. Moose did not change their use of the habitat categories among the three activity areas (all P-values > 0.05). However, they showed a tendency towards an increased use of coniferous forest in the post-disturbance area, 29 ± 5% compared to 17 ± 4% (Tukey: t-value = -2.2, df = 50, P = 0.08). The TRI of moose locations increased significantly from the pre-disturbance

Table 3. Differences in size of activity areas for adult female moose and adult female brown bears with and without offspring during the periods 27-50 hours prior to (the baseline area), 0-24 hours prior to (the pre-disturbance area) and 2-27 hours after (the post-disturbance area) a direct approach by researchers in helicopters in Scandinavia during 2003-2006, using paired t-tests.

Species	Comparison	N	t	df	P
Moose	Baseline area vs pre-disturbance area	77	0.920	76	0.360
	Pre-disturbance area vs post-disturbance area	77	-0.316	76	0.753
	Baseline area vs post-disturbance area	77	0.586	76	0.560
Bears with offspring	Baseline area vs pre-disturbance area	38	0.642	37	0.524
	Pre-disturbance area vs post-disturbance area	38	-0.746	37	0.460
	Baseline area vs post-disturbance area	38	-0.122	37	0.903
Bears without offspring	Baseline area vs pre-disturbance area	22	-0.514	21	0.613
	Pre-disturbance area vs post-disturbance area	22	0.718	21	0.481
	Baseline area vs post-disturbance area	22	-0.154	21	0.879

area (15.7 ± 12.1) to the post-disturbance area (17.0 ± 13.2; t = 4.0, df = 2,425, P < 0.01).

The bears neither altered their use of the habitat categories among the three activity areas (all P-values > 0.1), nor change their use of open or closed habitat in respect to helicopter disturbance ($F_{2,41}$ = 1.6, P = 0.2), and there was no difference in TRI between the pre-disturbance area (11.0 ± 8.9) and the post-disturbance area (11.3 ± 10.7; t = 0.34, df = 3,416, P = 0.73).

Discussion

Moose reacted to the helicopter approach with an immediate flight response, but not with a prolonged increase in their general activity. Adult female moose moved significantly longer than usual, up to two hours after the helicopter approach, but the size of the 24-hour activity area did not increase even though the distance between activity area centres increased and the overlap between consecutive activity areas decreased. Other ungulates have been reported to react similarly to helicopters. Based on three relocations separated by one day, Bleich et al. (1990) found that bighorn sheep *Ovis canadensis* moved 2.5 times farther the day following a helicopter survey than on the previous day and concluded that the animals took flight during or immediately after the disturbance. Contrary to our predictions, the bears moved relatively less than usual after helicopter approaches by researchers and thus reacted differently from moose. Bears did not change movement patterns the first hour after the approach, but bears without offspring moved less in the period 1-2 hours after the approach. Accordingly, bears did not change the size or overlap of the activity areas. Moose did not change habitat after being approached by helicopters, but they spent more time in rugged terrain and showed a tendency towards shifting to coniferous habitat. Thus, moose appeared to seek escape cover in rugged terrain and taller vegetation after being disturbed rather than moving longer distances. A similar effect was seen in Columbian black-tailed deer *Odocoileus hemionus columbianus* that fled into taller vegetation when approached by people (Stankowich & Coss 2007). Bears did not change habitats nor terrain after disturbance.

The difference in reaction between moose and bears to the helicopter approaches was the opposite of what we predicted, with the bears responding somewhat more calmly than moose. We suggest that the difference between moose and bears might be due to natural differences in the behaviour of members of different trophic levels (prey and predators). As such, moose and bears might perceive and, thus, respond differently towards danger even though helicopter disturbance should lack evolutionary reference in both species (Andersen et al. 1996). The moose, as a prey species, probably is adapted to immediate flight followed by seeking cover after exposure to risks, as we observed. Bears, however, react differently. If startled, they also quickly move away from the threat in the first minutes after exposure. Otherwise, they move slowly into cover to watch for danger, as documented when exposed to experimental meetings with hikers (Pedersen 2007). Hence, we interpret the reduced movement and lack of difference in use of terrain type before and after disturbance, not as being a lack of response in brown bears, but rather the result of tactical behaviour. The high variance in rate of movement by bears during the first hour after the encounter with the helicopter suggests that some animals may have been startled and ran a short distance before reducing their rate of movement.

The increased distance moved by moose the first hour after the helicopter approaches and the decreased movement by bears the second hour after the helicopter approaches was not influenced by the number of times the animals had been approached previously. Thus, given the intensity in our experimental design, no habituation or conditional behaviour was detectable. In Grand Canyon, USA, bighorn sheep displayed milder reactions to helicopter overflights once they became habituated to regular helicopter traffic (Stockwell et al. 1991). Individual moose and bears in our study were approached a maximum of four and seven times, respectively, over a period of 15 months, which is probably too infrequent to cause any habituation. Similar to mountain goats *Oreamnos americanus*, the reproductive status of moose did not influence the behaviour during the helicopter disturbance (Côté 1996, Goldstein et al. 2005). Female brown bears with cubs moved less than females without cubs both before and after approaches, which agrees with earlier findings that females with cubs restrict their ranges, perhaps to avoid contact with infanticidal males (Dahle & Swenson 2003). Helicopter disturbance has been found to have a seasonal effect on foraging efficiency in bighorn sheep

(Stockwell et al. 1991), but season did not influence moose movement in our study.

Our results indicate that using helicopters infrequently for short-term observations for research or monitoring purposes does not influence activity area estimations and movements based on GPS-based collection of positioning data for more than a couple of hours. However, moose showed a tendency to change their habitat use and changed terrain use. Even though this was not seen in bears, one should be cautious when using data from immediately after a direct helicopter approach in both species. The responses to helicopter approaches were apparently species dependent, implying that one should also be cautious when using knowledge from one species to predict the behaviour of other species or taxa.

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