

1 **Behavioral response of moose and brown bears to direct helicopter approach by**  
2 **researchers**

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24 **Abstract**

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

38 **Introduction**

39 Aircraft are frequently used in wildlife management and research projects on large  
40 mammals, because of the increased efficiency in data collection in the field. Large mammals  
41 normally have large home ranges and can be readily observed from low-flying aircraft  
42 (Jachmann 2002). Study populations of large mammals also often are found in remote areas,  
43 making helicopters a cost-efficient method and sometimes the only method available for locating  
44 and observing large mammals. For these reasons helicopters are frequently used in capture and  
45 radiomarking (Arnemo et al. 2006) and for monitoring and population estimation (Jachmann  
46 2002, Linklater & Cameron 2002) of large mammals. Although the potential for aircraft to alter  
47 wildlife behavior has been appreciated for many years (see Bleich et al. 1990 for review), direct  
48 approaches by researchers are used as a method for observing large mammals that already have  
49 been radio-marked (Solberg et al. 2006).

50 Approaching and low-flying aircraft may affect the behavior and ecology of wildlife. A  
51 range of species, from birds to terrestrial and marine mammals, react negatively to aircraft  
52 surveys and over-flights by e.g. increasing their movements and vigilance behavior, decreasing  
53 foraging efficiency by shifting habitat, and altering grouping patterns (Delaney et al. 1999,  
54 Linklater & Cameron 2002, Patenaude et al. 2002, Frid 2003, Southwell 2005, Tracey &  
55 Fleming 2007). Under certain conditions animals can become habituated to the disturbance  
56 (Miller & Gunn 1980, Stockwell et al.1991, Hughes et al. 2008), but the disturbance effects  
57 normally increase with increasing intensity of the harassment (Bayne et al. 2000, Goldstein et al.  
58 2005). The proximity and the direction of the aircraft in relation to the animals influence the  
59 effect of the disturbance, with more severe reactions by the animals to direct approaches and  
60 short distances to the aircraft (Stockwell et al.1991, Frid 2003).

61           The justification for disturbing animals in conservation, research, and management  
62 projects is sometimes questioned, thus for both ethical and scientific reasons, researchers should  
63 focus on animal welfare and know the effects of the necessary disturbances on the study animals  
64 and research results. Both short-term and long-term negative effects of capture on animal welfare  
65 have been documented in large mammals (Alibhai et al. 2001, Côté et al. 1998, Cattet et al.  
66 2008). However, there has been little attention to the disturbance effects of helicopter approaches  
67 in research projects (Scotton & Pletscher 1998). The effects of helicopter disturbance on large  
68 mammals have been documented for ungulates mostly from observing the animals during over-  
69 flights by helicopters in recreational or exploration traffic (Stockwell et al.1991, Côté 1996) and  
70 during aerial surveys (Bleich et al. 1990 and 1994, Linklater & Cameron 2002). The  
71 experimental overflights show that ungulates react more severely to threatening approaches  
72 (more direct approaches or at shorter distance) (Frid 2003; Goldstein et al. 2005; Tracey &  
73 Flemming 2007), but little is documented on the behavior in large mammals in response to a  
74 helicopter directly approaching a single focal animal during research projects. The effects of  
75 direct helicopter approaches on large carnivores have not yet been reported, even though routine  
76 helicopter approaches are used in many large carnivore projects.

77           To avoid biased results in wildlife studies using helicopters, it is essential to know if,  
78 how, and for how long an animal alters its normal behavior following the potential disturbance.  
79 Such knowledge includes not only the impact of the disturbance stimuli itself, but also a  
80 comparison of the animal's behavior in undisturbed and potentially disturbing conditions. This  
81 becomes even more important with the current transition from low-intensity data collection using  
82 VHF radio collars, to the high-intensity GPS-based data collection used in studies of large  
83 mammals, such as moose and brown bears (Moe et al. 2007, Dettki & Ericsson 2008). Until now

84 all studies investigating helicopter disturbance have used data from direct observations or low-  
85 intensity relocations of VHF radio-collared animals.

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

98 **Materials and methods**

99 This study was conducted in two areas in northern Scandinavia approximately 600 km apart.  
100 Moose were studied in the counties of Västerbotten and Norrbotten in Sweden and Nordland in  
101 Norway (65° 38' N, 15° 47' E; midpoint). The moose study area (23,000 km<sup>2</sup>) is characterized  
102 by boreal and mountainous forest that is dominated by Scots pine *Pinus sylvestris*, Norway  
103 spruce *Picea abies*, birch *Betula pubescens*, and willow *Salix* spp. This area is sparsely populated  
104 by humans (0.9 ± 0.8 inhabitants/km<sup>2</sup>) and has a low road density (220 m road/km<sup>2</sup>)  
105 (StatisticsSweden 2007). The average elevation is 1073 ± 464 m, and the mean temperatures in  
106 January and July are -13° C and 13° C, respectively. Snow cover lasts from the beginning of  
107 October until late May, and the vegetation period is about 110-130 days (Helmfrid 1996).

108 The bears were studied in Dalarna and Gävleborg counties, southcentral Sweden (61° 25'  
109 N, 14° 29' E). In the bear study area (4,363 km<sup>2</sup>) the rolling landscape consists of intensively  
110 managed boreal forest dominated by Scots pine or Norway spruce mixed with deciduous trees in  
111 earlier successional stages with a median average habitat patch size of 22,500 m<sup>2</sup> (Moe et al.  
112 2007). Although roads are common (929 m road/km<sup>2</sup>), the area is sparsely populated by humans  
113 (4.3 ± 2.1 inhabitants/km<sup>2</sup>) (StatisticsSweden 2007). The average elevation is 462 ± 170 m, the  
114 average precipitation is 600-1000 mm annually (Helmfrid 1996), and the mean temperatures in  
115 January and July are -7° C and 15° C, respectively. Snow cover lasts from late October/early  
116 November until early May and the vegetation period is about 150-180 days (Helmfrid 1996).  
117 Both moose and bears are intensively hunted in both the study areas.

118 Moose and bears were immobilized and equipped with GPS Plus neck collars with GSM  
119 lateral modems (Vectronic Aerospace 2003, for details see Arnemo et al. 2006). A location was  
120 recorded every hour for moose and every 30 min for bears. The locations were sent as text

121 messages containing packages of 7 locations to a database server using the digital cell phone  
122 network (Dettki et al. 2004). All incoming locations were reviewed for their validity, with only  
123 three-dimensional locations being used in the analyses. Following common guidelines for  
124 precision, we used only locations with a dilution of precision (DOP) value  $\leq 5$  in our analyses  
125 (IOC 2006) which resulted in a location omission of 21.5%.

126         Forty-six adult female moose (3-11 years old) and 17 adult female bears (3-12 years old)  
127 were approached in 2003-2007 by researchers in a helicopter to observe the animal to ascertain  
128 its reproductive success and survival, and some of the bears were approached to ascertain  
129 companionship with male bears for capture. Most individuals were disturbed more than once  
130 (maximum =7). Moose were approached both in the winter (October to March), when the ground  
131 was covered with snow, and in the summer (April to September), whereas the bears were only  
132 approached in the non-hibernating period (May to October). Approaches were omitted from the  
133 analysis when the focal animal or any accompanying animals were captured. The helicopter  
134 approached within 50-100 m of the focal animal only to allow visual observation and left as soon  
135 the status was determined, which typically lasted less than one minute. We noted the time the  
136 focal animal was observed from the helicopter.

137         We calculated the rate of movement (m/h) of the focal animals in 1-hour intervals using  
138 GPS positions. Due to occasionally lack of GPS reception, the movement rate was calculated  
139 between 2 successive locations with more than 1-hour difference in time, but with a maximum of  
140 a 2-hour time difference. All movement rates were assigned to the time of the latter position in  
141 the time interval. The rate of movement was compared with the rate of movement the previous  
142 day during the same hour of the day using a paired t-test. This was done to control for potential  
143 effects of circadian changes in movement of the moose and bears. Due to the occasional lack of

144 GPS reception, the sample sizes in our analysis varied. We compared the size of three different  
145 activity areas used by the animals before and after the approaches. The baseline area was defined  
146 as the minimum convex polygons (MCP) of the locations 27-50 hours prior to the approach, the  
147 pre-disturbance area was defined as the MCP of the locations 0-24 hours prior to the approach,  
148 and the post-disturbance area was defined as the MCP of the locations 2-26 hours after the  
149 approach. We separated the locations used for the activity area calculations by 2 hours, excluding  
150 the first 2 hours of immediate disturbance (the flight response) between the pre-disturbance area  
151 and the post-disturbance area, and a similar time gap between the baseline area and the pre-  
152 disturbance area. The 2-hour time gap between the baseline area and the pre-disturbance area  
153 was established to counter bias in the calculations of overlap between the activity areas.

154 We extracted Swedish Land Cover data (SMD) which is a raster with 25x25m pixels for  
155 each moose and bear location. We then reclassified the SMD categories and generated 4  
156 categories for bear habitat data (1: deciduous forest, 2: coniferous forest, 3: open pasture, 4: open  
157 young forest and open land). Due to differences in forage aspects, we separated open young  
158 forest and open land for moose data, and thus generated 5 categories. The SMD data for moose  
159 in Norway were not available and were excluded from the analysis. We also aggregated the  
160 habitat categories, by assigning categories 1 and 2 as closed habitat and categories 3 to 5 as open  
161 habitat. This was done to explore whether bears and moose shifted between closed and open  
162 habitat after being disturbed. We compared the topographic ruggedness index (TRI) for the  
163 locations in Activity areas 2 and 3. TRI is a measurement developed by Riley et al. (1999) to  
164 express the amount of elevational difference between adjacent cells of a digital elevation grid.  
165 The process essentially calculates the difference in elevation values between a center cell and the  
166 eight cells immediately surrounding it.

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

177           We fitted linear mixed models for TRI as a response variable with the explanatory  
178 binomial variable “before disturbance” (locations in the pre-disturbance area) = 0 and “after  
179 disturbance” (locations in the post-disturbance area) = 1 and the individual moose or bear as a  
180 random variable using the lme function in R (the nlme library) (R Development Core Team  
181 2005). TRI were log transformed prior to analysis to comply with the requirement of normality  
182 of the response variable in the models. The statistical packages R 2.0.1 (R Development Core  
183 Team) and SAS 9.1.3 (SAS Institute Inc., Cary, NC, USA) were used in all statistical analyses  
184 and the software ArcGIS 9.2 (ESRI, Redlands, CA, USA) in all GIS calculations. The  
185 significance level was set at  $p < 0.05$ .

186

187 **Results**

188 We approached the 46 female moose with helicopters a total of 88 times and the 17 female bears  
189 62 times. Most of the animals were moving away from the helicopter when observed. The moose  
190 were approached at  $12:00 \pm 2$  h (mean  $\pm$  SD) and the bears at  $13:00 \pm 6$  h. The average mean  
191 distance moved per hour in the 24-hour period prior to an approach was  $70 \pm 62$  m ( $n = 83$ ) for  
192 moose and  $352 \pm 284$  m for bears ( $n = 62$ ). We found no difference in the average mean distance  
193 moose moved in the 24-hour period prior to summer and winter approaches ( $t = -1.00$ ,  $df = 81$ ,  
194  $p = 0.32$ ,  $n = 57$  and  $n = 26$ , respectively), and there was no difference in the distance moved by  
195 60 moose with calves and 19 without calves ( $t = -0.52$ ,  $df = 77$ ,  $p = 0.60$ ). Bears with cubs ( $n =$   
196 21) moved less than bears without cubs ( $n = 40$ ) in the 24-hour period prior to the approaches (on  
197 average 151 m/h and 461 m/h, respectively,  $t = -5.46$ ,  $df = 59$ ,  $p < 0.01$ ).

198 During the first and the second hour after an approach, the moose moved on average ten  
199 times and three times farther per hour, respectively, than during the same hour the previous day,  
200 but this effect disappeared after 2 hours (Fig. 1, Table 1). Bears did not change movement  
201 patterns in the first hour after the approach, but contrary to moose, bears without offspring  
202 moved significantly less in the period 1-2 hours after the approach (Fig. 1, Table 1). The distance  
203 moved per hour by moose during the first hour after the helicopter approach was not influenced  
204 by the number of times the moose had been approached previously by helicopters, the season, or  
205 if the female was accompanied by a calf (Table 2). Bears were not influenced by the number of  
206 times they had been approached, but females accompanied by cubs moved less the second hour  
207 after the helicopter approach (Table 2).

208 The average size of the area used during the periods 27-50 hours prior to (the baseline  
209 area), 0-24 hours prior to (the pre-disturbance area), and 2-27 hours after (the post-disturbance

210 area) the helicopter approach was  $27 \pm 59$  ha,  $21 \pm 42$  ha, and  $23 \pm 34$  ha for moose ( $n = 77$ ),  
211  $220 \pm 396$  ha,  $302 \pm 632$  ha and  $237 \pm 393$  ha for bears with offspring ( $n = 22$ ) and  $974 \pm 1129$   
212 ha,  $853 \pm 854$  ha and  $1001 \pm 929$  ha for bears without offspring ( $n = 38$ ), respectively. We found  
213 no significant difference in size among the activity areas for either species (Table 3). In 63% of  
214 the 83 cases for moose, the baseline areas overlapped with the pre-disturbance areas, whereas  
215 only 32% of the pre-disturbance areas overlapped with the post-disturbance areas. The  
216 proportion of overlap was 77% and 68% for 22 bears with offspring and 68% and 68% for 38  
217 bears without offspring, respectively. For moose the distance between the centers of the pre-  
218 disturbance area and the post-disturbance area was on average 1237m and 44% longer than the  
219 distance between the centers of the baseline area and the pre-disturbance area (Paired t-test,  $t =$   
220  $2.2$ ,  $df = 76$ ,  $p = 0.034$ ). For bears these distances were not significantly different and were on  
221 average 1784m to 1431m (Paired t-test,  $t = 0.913$ ,  $df = 21$ ,  $p = 0.372$ ) for bears with offspring  
222 and 3537m to 3917m (Paired t-test,  $t = -0.819$ ,  $df = 37$ ,  $p = 0.418$ ) for bears without offspring,  
223 respectively.

224 SMD data were available for 33 individual moose and 59 approach events. Moose did  
225 not change their use of the habitat categories among the three activity areas (all  $p$ -values  $> 0.05$ ).  
226 However, they showed a tendency towards an increased use of coniferous forest in the post-  
227 disturbance area,  $29 \pm 5\%$  compared to  $17 \pm 4\%$  (Tukey:  $t$ -value =  $-2.2$ ,  $df = 50$ ,  $p = 0.08$ ). The  
228 TRI of moose locations increased significantly from the pre-disturbance area ( $15.7 \pm 12.1$ ) to the  
229 post-disturbance area ( $17.0 \pm 13.2$ ) ( $t = 4.0$ ,  $df = 2,425$ ,  $p < 0.01$ ).

230 The bears did not alter their use of the habitat categories among the three activity areas  
231 (all  $p$ -values  $> 0.1$ ), they did not change their use of open or closed habitat in respect to  
232 helicopter disturbance ( $F_{2,41} = 1.6$ ,  $p = 0.2$ ), nor was there any difference in TRI between the

233 pre-disturbance area ( $11.0 \pm 8.9$ ) and the post-disturbance area ( $11.3 \pm 10.7$ ) ( $t = 0.34$ ,  $df = 3416$ ,  
234  $p=0.73$ ).

235

## 236 **Discussion**

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

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

271           The increased distance moved by moose the first hour after the helicopter approaches and  
272 the decreased movement by bears the second hour after the helicopter approaches was not  
273 influenced by the number of times the animals had been approached previously. Thus, given the  
274 intensity in our experimental design, no habituation or conditional behavior was detectable. In  
275 Grand Canyon, USA, bighorn sheep displayed milder reactions to helicopter over-flights once  
276 they became habituated to regular helicopter traffic (Stockwell et al. 1991). Individual moose and  
277 bears in our study were approached a maximum of four and seven times, respectively, over a  
278 period of 15 months, which is probably too infrequent to cause any habituation. Similar to

279 mountain goats *Oreamnos americanus*, the reproductive status of moose did not influence the  
280 behavior during the helicopter disturbance (Côté 1996, Goldstein et al. 2005). Female brown  
281 bears with cubs moved less both before and after approaches, which agrees with earlier findings  
282 that females with cubs restrict their ranges, perhaps to avoid contact with infanticidal males  
283 (Dahle & Swenson 2003). Helicopter disturbance has been found to have a seasonal effect on  
284 foraging efficiency in bighorn sheep (Stockwell et al. 1991), but season did not influence moose  
285 movement in our study.

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

294

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305

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399

400 **Table 1.** Average speed (m/h) of adult female moose and adult female brown bears approached directly  
 401 by researchers in helicopters in Scandinavia in 2003-2006, and paired t-tests of differences.

Species	Minutes from helicopter approach	n	Average speed (m/h) (+/- SD)	Average speed (m/h) the same hour the previous day			
				(+/- SD)	t	df	p
Moose	-360 to -300	53	53 (102)	49 (84)	0.223	52	0.824
	-300 to -240	46	41 (83)	64 (204)	-0.717	45	0.477
	-240 to -180	51	57 (92)	156 (512)	-1.442	50	0.155
	-180 to -120	43	82 (221)	87 (226)	-0.103	42	0.919
	-120 to -60	51	29 (68)	54 (99)	-1.588	50	0.119
	-60 to 0	50	99 (181)	64 (92)	1.272	49	0.209
	0 to 60	41	467 (525)	46 (120)	4.873	40	0.000
	60 to 120	42	210 (296)	70 (169)	2.967	41	0.005
	120 to 180	51	180 (368)	105 (283)	1.137	50	0.261
	180 to 240	58	139 (251)	111 (257)	1.129	57	0.264
	240 to 300	68	91 (150)	86 (200)	0.165	67	0.870
	300 to 360	60	77 (105)	89 (203)	-0.439	59	0.662
Bears with offspring	-360 to -300	16	335 (449)	358 (487)	-0.128	15	0.900
	-300 to -240	17	70 (101)	80 (111)	-0.374	16	0.714
	-240 to -180	18	349 (668)	110 (235)	1.498	17	0.153
	-180 to -120	17	181 (438)	131 (289)	0.374	16	0.713
	-120 to -60	19	201 (311)	187 (358)	0.144	18	0.887
	-60 to 0	15	232 (324)	73 (83)	1.769	14	0.099
	0 to 60	14	242 (343)	182 (260)	0.493	13	0.630
	60 to 120	14	185 (418)	310 (417)	-1.287	13	0.221
	120 to 180	12	40 (23)	165 (361)	-1.190	11	0.259
	180 to 240	14	255 (588)	369 (597)	-0.964	13	0.353
240 to 300	13	441 (573)	321 (555)	0.491	12	0.632	

	300 to 360	13	200 (238)	386 (482)	-1.295	12	0.220
Bears	-360 to -300	39	310 (622)	435 (747)	-0.893	38	0.377
without	-300 to -240	35	549 (743)	448 (599)	0.998	34	0.325
offspring	-240 to -180	34	309 (539)	244 (417)	0.903	33	0.373
	-180 to -120	32	377 (743)	343 (608)	0.362	31	0.720
	-120 to -60	30	215 (405)	300 (600)	-1.148	29	0.260
	-60 to 0	24	221 (376)	240 (478)	-0.161	23	0.873
	0 to 60	20	575 (646)	540 (702)	0.154	19	0.879
	60 to 120	23	229 (395)	496 (644)	-2.501	22	0.020
	120 to 180	32	284 (512)	457 (674)	-1.125	31	0.269
	180 to 240	25	459 (708)	526 (903)	-0.315	24	0.755
	240 to 300	19	681 (803)	764 (1114)	-0.434	18	0.670
	300 to 360	24	410 (669)	612 (864)	-1.318	23	0.200

402

403

404 **Table 2.** Generalized linear mixed models of the effects of being accompanied by offspring  
 405 (Yes/No), season (summer or winter for moose) and number of times previously approached by  
 406 helicopter on the log distance moved per hour during the first hour for 43 adult female moose  
 407 approached 58 times, and during the second hour for 15 adult female bears approached 63 times  
 408 by helicopters of researchers in Scandinavia in 2003-2006.  
 409

Species	Explanatory variables	•	SE	<i>df</i>	<i>t</i>	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

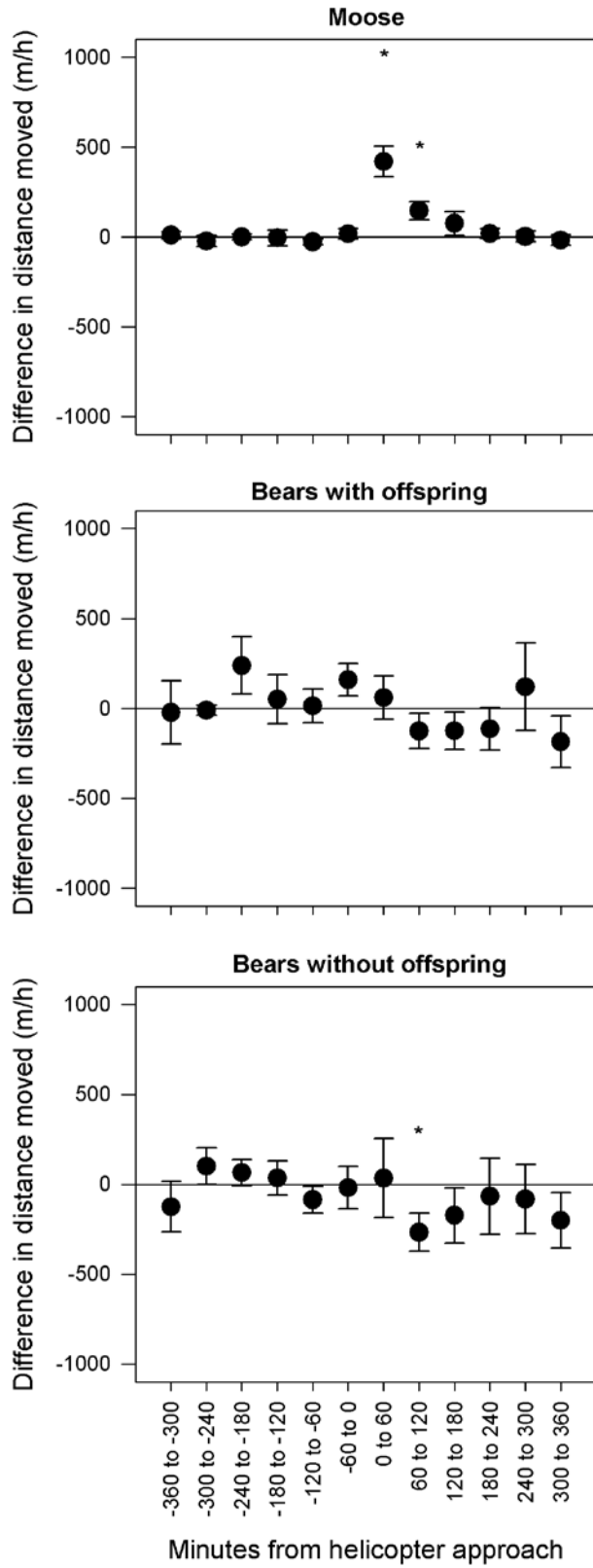
410

411 **Table 3.** Differences in size of activity areas for adult female moose and adult female brown  
 412 bears with and without offspring during the periods 27-50 hours prior to (the baseline area), 0-  
 413 24 hours prior to (the pre-disturbance area), and 2-27 hours after (the post-disturbance area) a  
 414 direct approach by researchers in helicopters in Scandinavia in 2003-2006, using paired t-tests.

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

415

416 **Figure 1.** Difference in distance moved ( $m \pm SE$ ) in adult female moose and adult female brown  
417 bears with and without offspring during 1-hour periods before and after direct helicopter  
418 approach by researchers in Scandinavia compared with the same hour the previous day in 2003-  
419 2006.



420

421 \* Statistically significant difference (paired t-test)