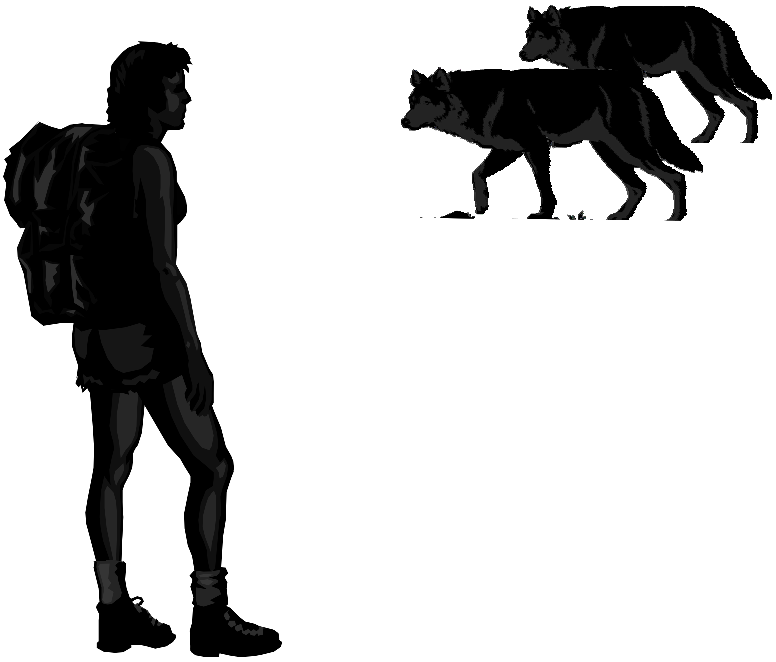
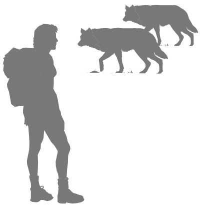
Wolf behaviour towards people



- the outcome of 125 monitored encounters

Cand. scient thesis

Hilde Karine Wam
2002



Wolf behaviour towards humans

– the outcome of 125 monitored encounters.

Ulv og menneske

– utfallet av 125 framprovoserte møter.

Hilde Karine Wam 2002

Cand. Scient. thesis
Cand. Scient. oppgave

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A heating warm day of July, somewhere in the countryside. Enclosed by dust-roads and barking dogs, a pack of wolves has settled for their day's rest in a small forest. The alpha male lies on top of a ridge, overlooking the stream valley below, where eight pups tumble naively around.
Suddenly he becomes aware the sound of wood being snapped under two feet, and he crawls out from the pine shadows. His yellowish eyes are blinded by sunlight as he stares motionless towards the sound. Then smell confirms; the only creature that can threaten his pack is on its way trough the forest.
A human is getting close…

FOREWORD

Thrilling! From the naive start of planning until getting it all down on paper, this thesis has consumed most of my time and energy, but I 'wouldn't trade it for the world'. Thank you, Olav, for giving me the opportunity!

And as always with field work, it was done not only by me: Carina R. Gustavsen, Olav Hjeljord and John-Gunnar Dokk were ready to approach wolves whenever I needed them. My special thanks to you, Carina, for all shared moments, for your everlasting smiles and for patiently criss-crossing every corner of wolf land under my directions!

We did not only intrude on the home grounds of wolves: Assar Alfredsson and Ole-Kristian Sauge without reservations shared their knowledge and equipment with us. My warmest thanks - you made things go a lot smoother. Also a helping hand was Mads Wiel who made possible several short-cuts for us. Without the holy key, we would still be out there!

My main thanks go of course to my supervisor Olav Hjeljord for both practical and intellectual support. Through him, my thesis was also financed by the SKANDULV project.

Finally, a big thank you to my sister for giving me the time. Without you, Hanne, I could not have spent all these days in the field.

Ås, 1st of December 2002

Hilde Karine Wam

SUMMARY

Wolves in the re-colonizing population of south-central Scandinavia were approached to test their tolerance to humans *per se* (N =125) 2001-2002. Five wolves were studied in two habitats with a different level of human impact. None of the radio-collared wolves or their 13-17 pack mates was ever aggressive, though an alpha female twice showed a behaviour with elements of defence at an early rendezvous (pup holding) site. In the other 123 trials, the wolf ran straight away. Mean tolerance distance (TD) was 257m, but varied considerably (47 - 488m) due to both environmental and intrinsic factors.

Of environmental factors, the wind contributed the most with TDs almost twice as long in a tailwind as in a headwind. While the effect of voice from the disturber (whether approached by one or two persons) was only slight, there was a stronger effect of noise from the ground in the path of the disturber.

Of intrinsic factors, the greatest effect was the influence of vulnerability. The alpha wolves were studied in two distinct periods of wolf vulnerability, i.e. with and without site-dependant pups. The wolves had longer TDs in trials when their pups were not able to follow the pack. The difference was a less for the wolf in the habitat with the strongest human impact. In one third of these trials, the alpha wolves returned to their bed site immediately after the disturber left the area. When the pups were able to follow the pack, however, the alpha wolves only returned when disturbed at a fresh moose kill. Overall, wolves stayed active for about eight minutes, and fled 325m. Differences between alpha wolves indicate an effect of the level of human activity within the wolf habitat. Also, pups at the age of 10 months behaved less determined than alpha wolves. This suggests the species has a high learning capacity.

Prior to being disturbed, the wolves used overlooking bed sites high in the terrain which may indicate a strategy to detect dangers before being surprised by them. After being disturbed, however, the wolves sought secluded sites, probably to hide from the danger.

I conclude that my study wolves were shy animals. This study also shows there is a marked difference in wolf behaviour between situations where the animal feel in control and not. This particular ability to judge a situation, and less respond to it by instincts, means there will be no fixed answer to how much aversive treatment is needed to keep the human fear in a wolf population.

Key words: Adaptation, *Canis lupus*, disturbance, fear, habituation, human, management, wolves.

SAMMENDRAG

Fra 2001 til 2002 gjennomførte jeg 125 forstyrrelsesforsøk på ulv i den reetablerende bestanden i Sør-Skandinavia for å teste adferden deres ovenfor mennesket *per se*. Fem individ ble studert i to habitat med ulik grad av menneskelig påvirkning. Ingen av de radiomerkede ulvene eller 13-17 flokkmedlemmer deres var noen gang aggressive, men ved to tilfeller viste en alfahunn tendenser til forsvar da hun ble forstyrret ved en rendezvous (valpeplass). I de 123 andre forsøkene stakk ulven umiddelbart av gårde. Ulvene flyktet på gjennomsnittlig 257m, men dette varierte sterkt (47 - 488m) som følge av faktorer både i ulvens omgivelser og i dyret selv.

Av ytre faktorer var vind av størst betydning med fluktdistanser nærmere dobbelt så lange i medvind som i motvind. Mens det kun var en svak effekt av forstyrrers stemmebruk (hvorvidt forstyrret av én eller to personer), var det en større effekt av bråk fra underlaget.

Av indre faktorer var det sterkest effekt av sårbarhet. Lederulvene ble forstyrret i to separate perioder av ulik sårbarhet, dvs. med og uten stedsbundne valper. Ulvene hadde lengre fluktdistanser i perioden da valpene deres ikke var store nok til å følge med flokken. Forskjellen var mindre for ulven i habitatet med størst menneskelig påvirkning. I ett av tre av disse forsøkene returnerte lederulven så snart forstyrrer trakk seg ut av området. Når valpene derimot kunne følge flokken, returnerte alfadyrene kun da de ble forstyrret ved et ferskt elgkadaver. Alt i alt var en ulv aktiv i omtrent åtte minutter, og flyktet 325m. Forskjeller mellom lederulvene indikerer en effekt av grad av menneskelig aktivitet i ulvens habitat. Videre oppførte 10 måneder gamle valper seg mindre målrettet enn voksne. Forskjellene mellom lederdyr, og mellom lederdyr og valper, antyder at ulv har en meget høy kapasitet for læring.

Liggeplasser brukt av ulvene før en forstyrrelse lå høyt i terrenget med god utsikt, hvilket muligens er en strategi for å oppdage og ikke bli overrasket av farer. Etter forstyrrelsen derimot oppsøkte ulvene liggeplasser i tette snar, sannsynlig for å gjemme seg bort.

Jeg konkluderer med at mine studiedyr var sky ulver. Studien viser også at det er klare forskjeller i ulvens adferd mellom situasjoner hvor den selv føler den har kontrollen og ikke. Denne evnen til å vurdere en situasjon, og i mindre grad reagere instinktivt på den, betyr at det ikke er noe fasitsvar på hvor mye avskremming som må til for å beholde en ulvebestands skyhet.

Stikkord: *Canis lupus*, forstyrrelse, forvaltning, frykt, menneske, tilpasning, tilvenning, ulv.

CONTENTS

I. INTRODUCTION

We all know what happened to Little Red Riding Hood when she met the Wolf in our childhood's fairytale. Despite her fate though, we are split in our view of how dangerous the **real** wolf *Canis lupus* is: about half of all Scandinavians asked express a fear for wolves (Karlsson *et al.* 1999, Bjerke & Kaltenborn 2000). Also in other areas of the world where the wolf is re-colonizing, 40 - 50% of the people fear the animal (Kanzaki *et al.* 1996, Lohr *et al.* 1996, Bath 2000, Bath & Majic 2001).

Since our opinions so much diverge on these matters, we obviously are in need for more knowledge. People want to know what to expect from the mythic animal that few have experienced other than on photos. Is it like grandparents have told the generations, that if we happen to encounter 'the mighty beast, only a great effort with sticks and stones can save us from its snarling white canines'? Or will it simply tuck its tail, and disappear without us ever knowing it was there? Myths are exaggerated stories, and they tend to create like-wise counter-responses. Clearly there is a need for facts!

From the historical records we **do** know that gray wolves can attack and even kill people. Linnell & Bjerke (2002) provides an up-dated summary of wolf attacks on humans. In their report they conclude that historically there are four situations where wolves have been known to attack: rabid wolves, habituated or hybrid wolves, wolves lacking natural prey and specific cases where a human have cornered the wolf. The report is a solid documentary showing the historical relationship between wolf and man. And from its contents, we can outline precautions to minimize future attacks.

However, the wolf undoubtedly is one of the most adaptive mammals on earth. Physiologically the species stays the same, but its **behaviour** may still change rapidly (see e.g. Bibikov 1982, Boitani 1982, Mech 1989, Promberger *et al.* 1997, Merrill 2000). Factors likely to induce a response in the wolf's behaviour towards people, are changes in the hunting pressure, the prey availability or the human activity within its habitat. In most areas where wolves presently are re-colonizing, one or more of these changes **have** taken place. Accordingly, wolves today might be more or less fearful of man than their ancestors were.

Before we can outline any precautions concerning wolves, we have to know our starting point. I therefore report on the outcome of 125 monitored encounters between wolf and man, achieved by approaching radio-collared wolves on their bed sites. With the data obtained I evaluate to what extent the wolves actively avoided human contact. I also test the influence of several factors (see hypotheses) that affected their behaviour. Finally, I use both the wolves' behaviour and their choice of bed sites to look for eventual adaptations they have made to living in a human world.

Only by observing the behaviour of wild wolves in their natural environment, will we be able to monitor the eventual process of their habituation to people. With that in mind, I went out to meet the mythic animal

HYPOTHESES: What will affect the wolves' behaviour?

THE ENVIRONMENT: EXTERNAL FACTORS

I. Wind

The direction of wind will affect when wolves detect approaching humans, since it affects the level of scent molecules that reaches the wolves. Therefore wolves will react at a longer distance in a tailwind than they will in a headwind. Accordingly, the wind strength will amplify these differences.

II. Sound

Since two people in a conversation make more vocal noise than one walking alone, wolves will react at a longer distance when approached by two persons. As for the wind strength, increasing levels of noise will amplify any differences. Also, there is likely an effect of ground noise from the path of the approaching person. Such noise may alert the wolves before the human scent reaches them.

THE INDIVIDUAL WOLF: INTRINSIC FACTORS.

I. Exposure to people.

Wolves more frequently exposed to people may habituate, or they may become more fearful. Hence, wolves living in a habitat with higher levels of human activity, will react at other distances than wolves in a more pristine environment. Also, since older wolves previously have encountered people, they will behave more controlled and determined than younger ones when disturbed.

II. Vulnerability to humans.

With site-dependant pups nearby, alpha wolves will be more on guard. Accordingly, they will react at a longer distance when approached in the vicinity of such pups, though the wolf may not flee at a longer distance. As the pups grow old enough to follow the pack, the alpha wolf no longer has this incitement to be more on guard.

II. MATERIAL AND METHODS

i. Study area and wolves

I studied wolves in two separate territories 30 km apart in south-central Scandinavia (Fig. 1), each representing a different level of human activity. Moss -Våler is a habitat with stronger human impact, relative to Årjäng – Kongsvinger[1] (see Table 1, next page for details). Since the level of human impact is the only difference between these two territories, it provides a unique possibility to study individual habituation in wolves.

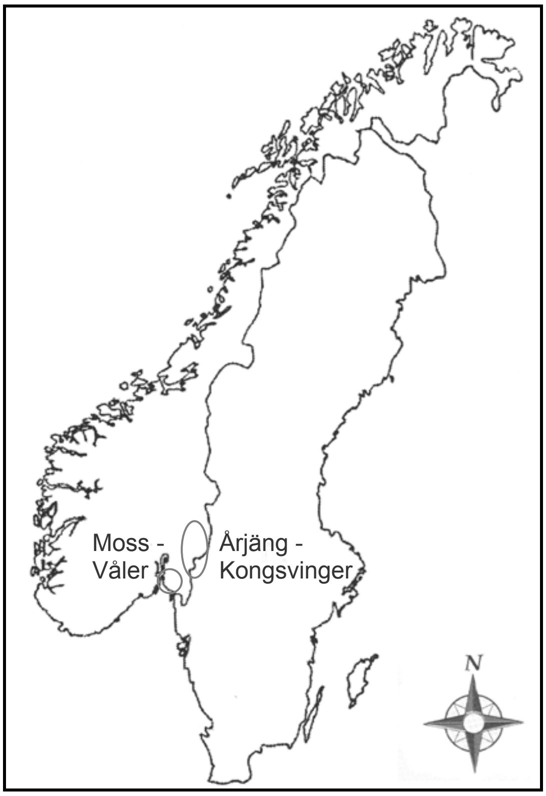

FIGURE 1. *The location of two wolf territories in south-central Scandinavia, where gray wolves were approached by a person to test their tolerance to humans, 2001-2002.*

The habitat

The Rømskog territory covered a 1600 km² area along the border of Norway and Sweden (59˚32' - 60˚08' N), while the Våler territory covered 550 km² on the Norwegian side (59˚21' - 59˚40' N). Within the Våler territory, there are about 12 times as many people living, and 40 times as much cultivated land, as there are in the Rømskog territory (Table 1).

The territories consist of mixed conifer-deciduous boreal forest, with more deciduous in Våler, and a gently rolling topography at 25 - 255 m.a.s. in Våler, and 130 - 430 m.a.s. in Rømskog. However, the terrain in Våler is rugged on a finer scale than Rømskog. In both territories the wolves have abundant wild ungulate prey.

The wolves

I studied five radio-collared wolves (Table 2, next page). Apart from these individuals, no other wolf in either territory was radio-collared. All the radio-collared wolves in the study have been captured by darting from helicopter.

Concerning hunting pressure, I consider the wolves to have the same historical background. After severe eradication efforts that started in the 19th century, wolves were functionally exterminated from the Scandinavian peninsula by 1966 (Wabakken *et al.* 2001). The population of wolves that presently re-colonizes the area, are all descendants of two or three animals that apparently migrated from Karelia, Finland 10-25 years ago (Vilà *et al.* 2002). The Karelian population has been hunted continuously by man since pre-historic times (Pulliainen 1965).

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[1] To avoid repeating the lengthy names in the text, I have called the two territories 'Våler' and 'Rømskog' after their core area.

TABLE 1. *Level of human impact in two Scandinavian territories where wolves were approached by a person to test their tolerance to humans, 2001-2002. Våler was selected as a habitat with stronger human impact, relative to Rømskog. Data from National Survey Maps 1: 50 000 (1996).*

	Density per km^2		Percentage of land		
Territory	**Humans**	**Public roads**	**Cultivated**[1]	Forest	Open water
Rømskog	1,8	0,2	0,9	90,0	9,1
Våler	22,1	0,5	36,9	59,2	3,9

[1] Including agricultural land and areas of human settlement

Hence, my study wolves have all had the same evolutionary incitement to avoid people, and become shy animals. There has been no **legal** hunting of wolves in Scandinavia after they became a protected species in 1966 (Sweden) and 1972 (Norway). However, to eliminate their litter of hybrid pups, the Våler pack was intensively chased by an official hunting team for two months in the spring 2000. Although not evidentially confirmed, there is reason to assume that the wolves in both territories are subject to the same level of **illegal** hunting (*).

TABLE 2. *Selected animals in a behavioural study where gray wolves were approached by a person to test their tolerance to humans, south-central Scandinavia 2001-2002.*

Wolf	Sex	Year born	Weight (kg)	Habitat	Social status	Pack members at the time of study
9808[1]	♂	1997	xx	Våler	Alpha*	Alpha ♀, 1-2 subordinates, 8 pups 2001.
0001[1]	♂	1993-94	52	Rømskog	Alpha*	0002, 2-4 subordinates, 3 pups 2001 (0209,0211)
0002[1]	♀	1993-94	40	Rømskog	Alpha	0001, 2-4 subordinates, 3 pups 2001 (0209,0211)
0209[1]	♀	2001	34	Rømskog	Pup	Living solitary at the time of experiment.
0211[1]	♀	2001	31	Rømskog	Pup	Partly solitary. Alone at the time of experiment.

[1] Number in the Skandulv files (a Scandinavian wolf research group).

* The wolf 9808 vanished from the territory in November 2001, and the wolf 0001 in April 2002.

ii. Field work

a. Locating the wolf

Prior to each trial, I located the wolf using standard telemetry methods from the ground (i.e. triangulation, see Kenward 1987). I triangulated only when wolves were completely at rest, and if a wolf moved, I started the triangulation process all over again. To minimize bias between personnel, I located all wolves throughout the study. A second person assisted, but did not triangulate independently prior to a trial.

I classified accepted position fixes as quality III, II or I based on accuracy. A fix was accepted if any three out of the first four bearings (Fig. 2A and 2B) crossed less than 0.5 mm (quality III), 1.0 mm (quality II) or 1.5 mm (quality I) apart on a 1: 50 000 map (a quality I fix was only accepted if it could be checked on snow afterwards). If more than one of the first four bearings crossed wider apart than 1.5 mm (Fig. 2C), I did not accept any of these bearings, and started a new triangulation.

When the approached wolf was moving after it had left its bed site, I determined its position using two bearings only. When it rested again, its new bed was determined as in Fig. 2. Before analysing the data, I found the exact wolf positions using the same map in 1: 25 000.

b. Accuracy of triangulations.

I tested the accuracy of my triangulations as follows: During periods with snow, I checked all locations with a Garmin 12 GPS by searching for, and following the wolf tracks after a trial. The accuracy of the GPS itself is stated to be 15 m (Garmin Corporation 1999), although in field it rarely indicated an error value above 8-9 m (only under very dense spruce *Picea abies).* In addition, I made two test series of arranged trials. Based on this material, I estimated the mean error for each of the three triangulation qualities III, II and I (Table 3):

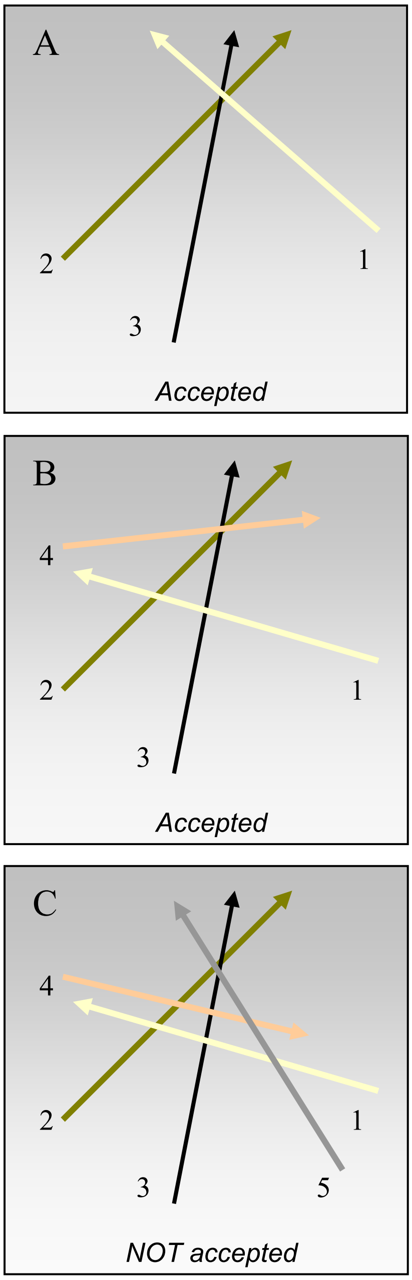


FIGURE 2. *Criteria for accepting telemetry fixes of wolves in a study of their tolerance to humans, Scandinavia 2001-2002. At least 3 bearings had to cross <1,0 mm apart (1,5 mm when it could be checked on snow) on a 1:50 000*

TABLE 3. *Total number of locations and accuracy in triangulations of gray wolves in a study of wolves' tolerance to approaching humans, south-central Scandinavia 2001-2002.*

	Quality III	Quality II	Quality I [1]
Total no. of wolf locations in the study	**92**	**27**	**6**
a. No. of total locations checked on snow	16	6	6
b. No. of locations in separate test trials	9	3	2
Mean error (m) based on a. and b.	±20	±37	±50
SD of error (m)	7	5	10

[1] A quality I fix was only used in the study if it could be checked on snow afterwards.

Note that the estimated accuracy is only for positions when the wolf lay still at its bed site. The wolves in this study usually rested on small and local hill-tops (see later chapters), which probably improved the accuracy of a triangulation (Kenward 1987). Triangulations taken during wolf movement both have a higher and a more variable mean error. I estimate it to be up to 150 m at worst, depending on topography, and the speed at which the wolf is moving.

The same telemetry equipment was used on the respective wolves throughout the study period. Wolf 9808 had a Telonics radio collar, and was located using a Telonics TR-2 receiver. A TeleVilt RX-89 10 receiver was used in supplemental positioning, but never alone. The other wolves had Advanced Telemetry System radio collars, and were located using ATS FM-100 receivers.

c. Approaching the wolf

After a wolf was located, I monitored the animal from a hill-top 600-800 m away, while another person approached it. To determine whether the wolf first moved **away from** or **towards** the approaching person, the angle between us was kept at ~ 90°. We communicated by radio. Fig. 3 (next page) illustrates the setting

The person who approached the wolves, hereafter called the disturber, started off at about twice the distance at which I expected the animal to respond (½ -1 km). Care was taken so that the wolf had a free choice of moving in all directions, i.e. if it was close to a road, field or river, the disturber approached it parallel to this, and not at an angle which would lock the wolf in between. The disturber walked straight towards the wolf in a normal hiking behaviour, being one or 'two' persons ('two' means simulating a conversation between two). The disturber was either a female (175 cm, 60-65 kg), or a male (190 cm, 80-85 kg).

The disturbers were temporarily stopped at every sign of the wolf making a move, and then recorded their own position using GPS. During the study it became apparent that a wolf not always moved away from its bed site immediately after showing the first sign of responding to the approaching person. Typically then the radio-signal briefly (about 10 seconds) indicated activity, as if the animal only changed its body position. Usually the signal became **stronger** before it went back to stable.

When the wolf finally left its bed site, the disturber remained at the stop position until the animal rested again. Thereafter she or he withdrew in the same track as they had approached the wolf. Though, a movement ± 50 m from the stop was allowed to avoid losing the radio-signal, **after** I could confirm that the wolf had left in the opposite direction. To test how it affected the wolves' behaviour, in 10% of the trials the disturbers did not stop, but proceeded even after the wolf had left its bed. On these occasions they continued to walk in their original direction, and did not 'follow' the wolf.

When the wolf left its bed, its movements were recorded by me and the disturber using separate receivers, and the time was taken until it bedded again on a new site. With synchronized watches we took one bearing after half a minute, 1 minute and thereafter every 2. minute as long as the wolf was active. In some trials we were not able to take all the bearings, usually due to the disturber being too low in the terrain to receive the radio-signal.

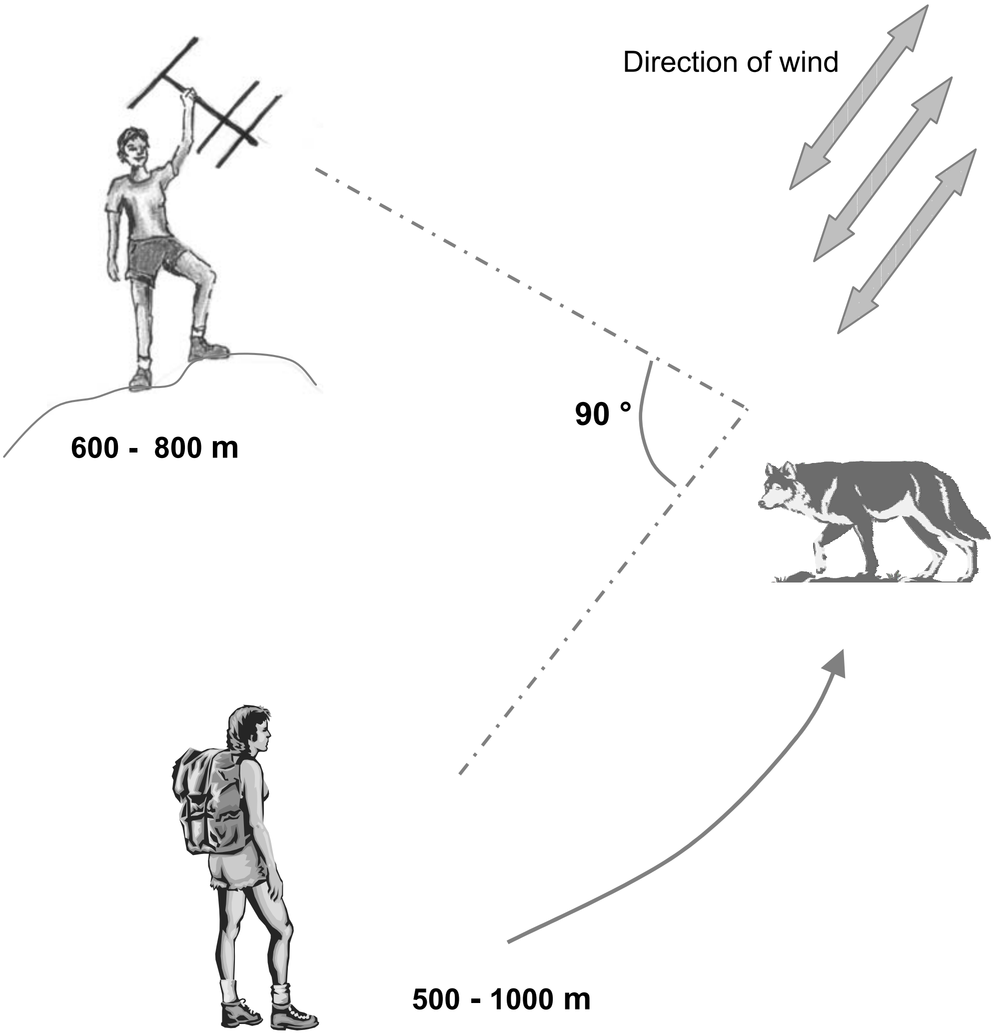


FIGURE 3. *The setting of a an experiment where gray wolves were approached by a person to test their tolerance to humans, south-central Scandinavia 2001-2002.*

Five different behaviour patterns were measured during each trial:

a. The **sensing distance**, i.e. the distance at which the wolf first showed a response to being approached (the temporary increase in strength of its radio-signal).
b. The **tolerance distance,** i.e. the distance at which the wolf finally left its bed site.
c. The **waiting distance**, i.e. the difference - if any - between a sensing distance and a tolerance distance in the same trial.
d. The **fleeing distance**, i.e. the linear distance which the disturbed wolf moved between its original and new bed sites.
e. The **time spent active**, i.e. the time passing from a wolf left its original bed until it rested again on the new.

To test short-time effects of disturbing the wolves, an animal was approached once, twice or three times on the same day. All conditions were kept the same in these **repeated trials**, and the next trial was started when the wolf had been resting one hour at its new bed site.

We disturbed the alpha wolves in two distinct periods; with and without site-dependant pups. I considered pups no longer site-dependant when they started to follow the pack (medio September, pers.obs.). **The distinction was made to reflect different vulnerability of the pups, which I expected would influence the behaviour of the alpha wolves.** The two pups were studied at the age of 10-11 months, and only when it could be confirmed that no other wolves were in their vicinity. In both periods, and for all individual wolves, trials were repeated an equal number of times under similar conditions regarding the wind and whether the wolf was approached by one or 'two' persons. Wind conditions were categorized as headwind, no wind or tailwind, with head- and tailwind further categorized as either strong, middle, or weak. In the analyses, however, I have not distinguished between the different wind strengths, as the differences were only slight.

Ethical note: No trials were done during the denning season. In early and mid summer, when the wolves were at their first rendezvous sites, the disturber withdrew immediately to avoid causing the wolves to abandon the site. In the few trials where the disturber proceeded after the wolf left, it was a pre-requisite that site was not a rendezvous.

d. Characteristics of the wolves' bed sites

At the wolves' bed sites I registered these parameters: terrain level, field of vision, vertical cover and canopy coverage (Table 4, next page). The first two parameters supposedly reflect the wolf's chance of detecting other animals (including an approaching person), and the last two reflect its chance of self being detected.

When I did the registrations, I crouched to record the data at the shoulder height of a wolf. In the analyses I used only quality III bed sites (triangulated to ± 20 m) since the site parameters can change substantially at a short distance.

iii. Statistics

All analyses are run in Minitab version 13 (Minitab Inc. 2000). Significant results are marked *** ($p \leq 0.001$), ** ($p \leq 0.010$) and * ($p \leq 0.050$). Results were considered not significant if $p > 0.050$. To make it simply, I quote the test's name

TABLE 4. *Habitat parameters that were measured on bed sites for gray wolves in a study of their tolerance to humans, south-central Scandinavia 2001-2002.*

Habitat parameter		Scale	Measurement
To detect	Terrain level	0-100 %	Measured at the local scale. Percentage of land located below the wolf bed, considering only visibly connected land extruding from the bed. At 100% wolf looked down on all surrounding terrain.
	Field of vision	Metre	∑sight distances in all directions (north+south+east +west). I used mean values for each direction. E.g. to the north, a wolf could see 80% 20 m, 10% 2 m and 10% 107 m, thus, the sight value for north would be the average 27 m.
To hide	Vertical cover	0-100 %	The percentage of field of vision obstructed by objects within $r = 18$ m around the bed site, i.e. vegetation, rocks etc. 100 % thereby corresponds to a field of vision ≤ 18 m in all directions.
	Canopy coverage	0-100 %	Within $r = 18$ m around bed site. The projected cover from the above tree canopy down on the ground. 100 % means full cover, 0 % no cover.

once in each chapter, e.g. Kruskal-Wallis $H = 3.12$, and thereafter only the test statistic, i.e. $H = 3.12$.

I used Anderson-Darling to check if data were normally distributed, and Levene to check for equal variances. I then used the combination of these to determine whether data samples were symmetrical, which is crucial to the choice of non-parametric tests. In the final analyses, I grouped data for the alpha pair in Rømskog whenever initial tests showed no difference between them. Likewise, I grouped data for the two pups. I treated trials where study wolves were together (alpha pair in Rømskog) as dependant, though, and omitted one set when calculating overall mean/median and variances/quartiles.

The sensing and tolerance data both fit the assumptions of normality, so I used MANOVA to test for effects of variables. For significant effects, I later used Tukey's confidence limits to pinpoint the differences. Prior to the field work, I had chosen the factors individual, period, wind and the number of persons disturbing to frame a balanced design for the MANOVA analysis. During field work, I also made correction marks in trials which could have been influenced by other factors; ground (more or less noisy than average) topography (a hill blocking the wolves from smell and noise made by the disturber) and vision (sight from the wolf's bed site in the direction of the disturber was longer than the mean tolerance distance for trials with otherwise equal conditions). I 'tested' for effects of these factors by checking against confidence interval and unusual observations in the MANOVA.

The fleeing distances, the time spent active and most habitat characteristics were highly skewed, so I analysed them using non-parametric methods (no transformation was done to make any data normal). I used Mann-Whitney to test for differences between individuals and periods wherever a Kruskal-Wallis suggested there was one. I used paired Wilcoxon Sign Rank or paired Student-t to test for differences in bed sites before and after a trial when data were symmetrical. If not symmetrical, I used a paired Sign test.

Tests were done one-sided whenever appropriate. Any measures I give of variance are standard deviation if not otherwise indicated.

TABLE 5. *Number of trials in a behavioural study testing the tolerance of gray wolves to approaching humans, south-central Scandinavia 2001-2002.* [1]

Period	Alpha wolves			Pups	
	9808	0001	0002	0209	0211
1. Pups at rendezvous sites June/July	18	18	18	-	-
2a. Pups travelling with pack Sept/Oct	18	-	-	-	-
2b. Pups on their own within the territory Jan/Feb/Mar/Apr	-	18	18	9	8
∑ trials = 125	36	36	36	9	8

[1] A detailed list of the trials is given in Appendix A.

III. RESULTS

From June 2001 to May 2002, we approached the wolves a total of 135 times. Due to technical problems ten trials were not accepted. Trials done on the alpha wolves were equally distributed between the two periods of different pup vulnerability, while the pups were studied at the age of 10-11 months (Table 5).

The results are organized in three parts: The first part covers the distances at which the wolves reacted when approached, and what factors they responded to. In part two, I show **how** they behaved, i.e. whether they moved towards or away from the disturber, how they moved in relation to wind, how far and for how long they moved before settling again, and also whether they came back. In the last part I compare the wolves' bed sites used before and after a trial.

i. At what distance did the wolves react?

a. Their sensing distances.

In one quarter of the trials, the radio-signals indicated the described brief activity, which I called the wolf's sensing distance, some time before the wolf started to move away from its bed site. I recorded this behaviour on the same number of days with a tailwind (10) and no wind (10), but fewer when there was a headwind (6). Also, there were fewer registrations of a sensing distance for the pups than for the alpha wolves, as I recorded the behaviour in 39% of the trials done on the Våler male, 30% on the Rømskog pair, but in only 17% on the pups.

b. Their tolerance distances.

The wolves left their bed sites when the person who approached them was 47 - 488 m away (Fig. 4, next page). Both intrinsic and external

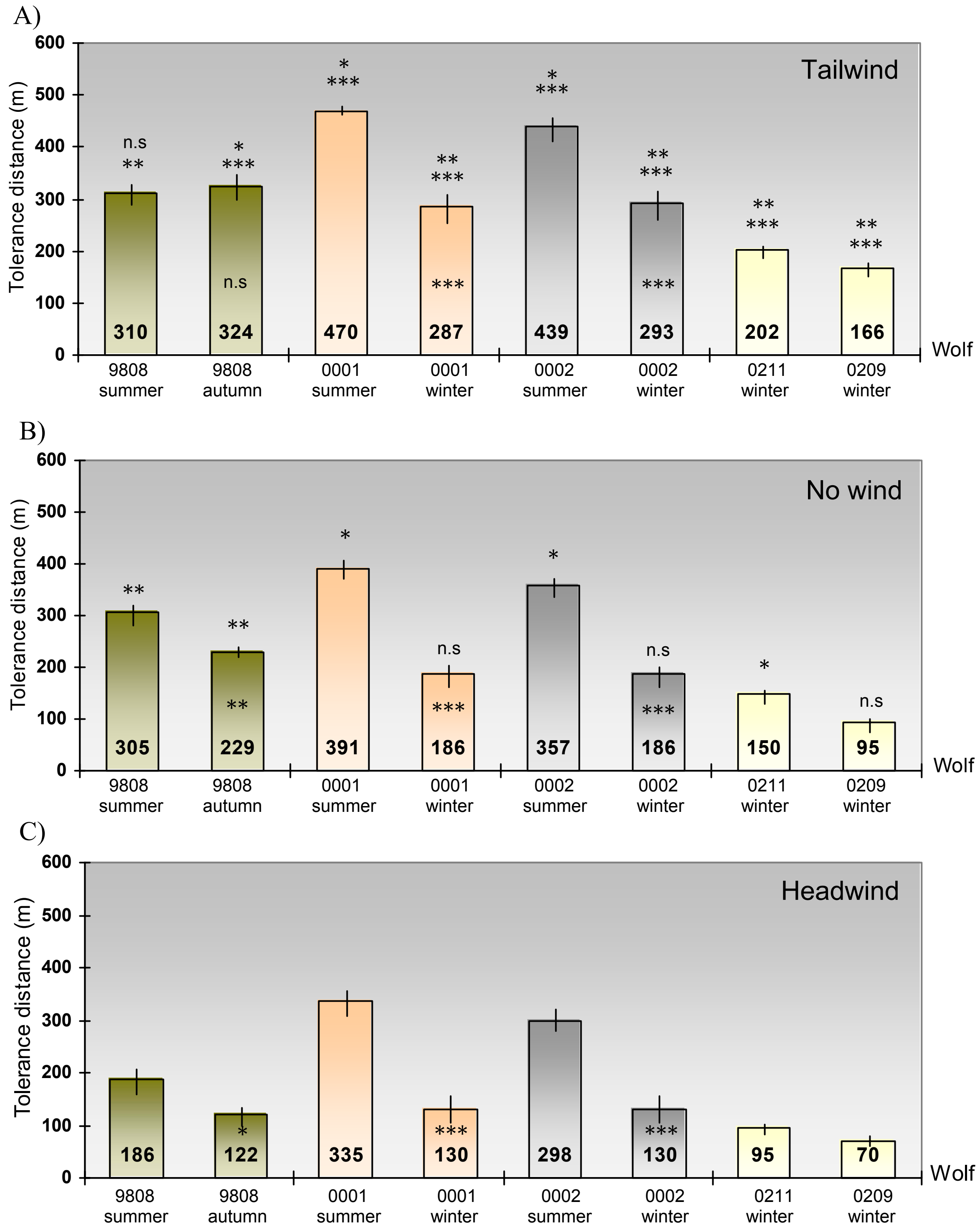


FIGURE 4. *Mean tolerance distance ± SE for gray wolves approached by humans, south-central Scandinavia 2001-2002 in different wind directions and in two different periods; with and without mobile pups. N =125. Significances indicated on bars are for periodical differences (same wolf and wind), while those above bars are for wind directions (same wolf, same period): in A) the uppermost row of significances are between tailwind (A) and no wind (B), while the row below are between tail- (A) and headwind (C). In B) the significances are between no wind (B) and headwind (C). Wolf 0001, 0002 (alpha pair), 0211 and 0209 (pups 10-11 months old) belonged to the same pack, while 9808 was alpha male in a territory with a relatively higher human impact.*

TABLE 6. *Factors affecting the tolerance distances of gray wolves when approached by a human, south-central Scandinavia 2001-2002. The wolves were studied in two different packs, and pups were studied at the age of 10-11 months. N =125.*

Factor	Level	Test results [1]	
		F	*P*
Individual	Våler alpha male Rømskog alpha male Rømskog alpha female Rømskog pups	6,96	0.000 ***
Period	With site-dependant pups Without site-dependant pups	99,11	0.000 ***
Wind	Tailwind No wind Headwind	44,25	0.000 ***
Sound	One person Two persons	7,99	0.005 **

[1] MANOVA

factors (Table 6) significantly influenced this ten-fold span in the wolves' tolerance distances (TD).

Influences from the individual wolf.

There was an effect of the individual wolf on the TDs, but not all five wolves differed from each other in this respect: For the alpha wolves, the effect was significant only during the first period (the rendezvous period), when the Våler male had shorter TDs than the Rømskog pair (mean 267 ± 84m Våler versus 385 ± 85m Rømskog) (Tukey's *t* =3.27, 106 df, *P* =0.004). In the second period they had the same TD (mean 225 ± 102 versus 202 ± 101), which were significantly longer than for the pups (*t* = -4.15, 123 df, *P* =0.000). The differences hold for all wind directions, and whether disturbed by one or 'two' persons.

Influences from period.

In the second period, all the three alpha wolves had shorter TDs than during the first period (mean 210 ± 101m versus 346 ± 101m), except the Våler male in a tailwind (Tukey's *t* = -0.37, *P* =0.691). The Rømskog pair had TDs that were 42% (headwind), 50% (no wind) and 64% (tailwind) of what they had been during the first period (Tukey's *t* = -3.83, *P* =0.001), while the TDs for the Våler male were reduced to 66% (headwind) and 75% (no wind) (Tukey's *t* = -2.11, *P* =0.045) (Fig. 4).

Influences from wind.

Apart from the effect of period, the wind was the most significant contributing factor in the MANOVA analysis (Table 6). The trend was clear for all individuals: compared to when there was no wind, they had longer TDs when there was a tailwind, and shorter when there was a headwind (Fig. 4). The overall mean TD (all wolves, both periods) were 329m in a tailwind, 259m when no wind and 184m in a headwind.

Influences from sound

For all wolves taken together in the MANOVA, the TDs were influenced by whether disturbed by one or two persons (Table 6). Taken individually, however, there was a significant effect only for the Våler male in a tailwind (Tukey's t =2.98, P =0.003). There was also an effect of noise from the ground: 44 trials had been marked for abnormal ground conditions (24 less noisy, 20 more noisy), e.g. bogs, logging waste, crisp or wet snow etc, of which 28 had TDs outside the 99% confidence interval (Fig. 5).

Fifteen of these 28 trials were marked for a **less** noisy ground, had lower TDs than expected, and were all in a headwind on wet snow in Rømskog. The remaining thirteen trials were marked for a **more** noisy ground. They were all for logging waste, and had longer TDs than expected. Also, six trials marked for a more noisy ground **coincided with a SD registered** (including only two of the trials in Fig. 5).

Influences from topography

One of the unusual TDs in the MANOVA coincided with a topographical correction (see *Statistics*) I had made, while another coincided with a correction mark for field of vision (both for the Rømskog pair). I had made two more corrections, both for the pups (vision, for details see *Statistics*), but these did not differ from the overall mean. Hence, the sight of a person triggered a fleeing response in the adult wolves, but not in the young ones.

Influences from repeated trials.

When approached twice in a row, the wolves' TDs the second time did not differ from the first (N =14, paired t = 2.27, P =0.770).

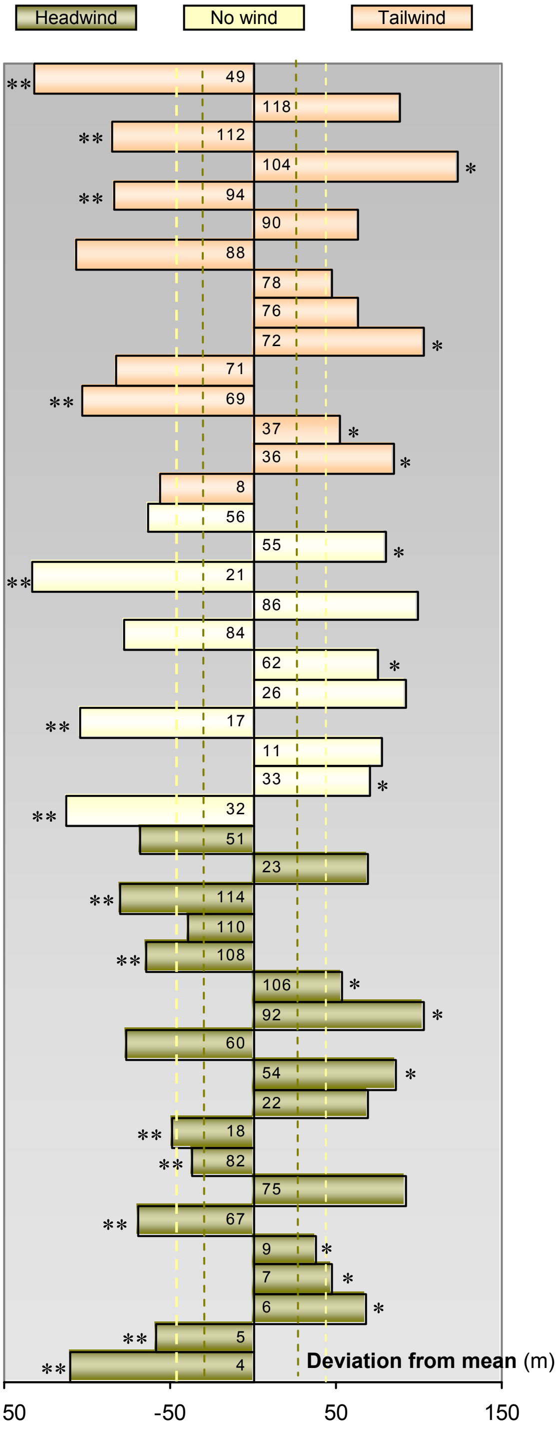


FIGURE 5. *Deviations from the mean tolerance distance of wolves approached by humans, Scandinavia, 2001-2002. The yellow dotted line is a 99% CI for trials in tailwind or no wind, the green line for headwind. Trials marked with * had a more, or ** less noisy ground than normal. The number on each bar is trial no.*

c. Their waiting distances; the relation between sensing and tolerance.

On average a sensing distance (SD) was 56 ± 19% longer than the corresponding tolerance distance (TD). The SDs did not differ between the alpha wolves (*F* =1.31, 2 df, *P* =0.781). Recall that the difference between a SD and a TD is what I called the waiting distance.

While the SDs are correlated with the TDs (N =26, Pearson's ρ = 0.697, *P* =0.000), **the waiting distances are negatively correlated** with the TDs (ρ = -0.651, *P* =0.000), i.e. with longer TDs, there was a shorter lapse between sensing and tolerance (Fig. 6). Also, the pups had about 10% longer waiting distances than the alpha wolves, but with only three SDs registered for the pups, this could be pure chance.

Since the waiting distances are correlated with the TDs, they were affected by the wind (*F* =17.20, 21 df, *P* =0.000). The waiting distances were significantly shorter in a tailwind, and greater in a headwind (Tukey's confidence mean 293 ± 193 m headwind versus 141 ± 44 m for tailwind), though it varied more when there was a headwind. The waiting distance was not affected, however, by whether the wolf was approached by one or two persons (*F* =1.89, *P* =0.184).

ii. How did the wolves behave?

How the wolves behaved after being disturbed from their bed site, is difficult to quantify. I have given it a descriptive treatment. The fleeing distance and the time a wolf spent active, however, can both be quantified, and I have used these measures to test for differences between individuals and periods.

The fleeing distance and the time a wolf spent active are not correlated with the tolerance distance (N =126, Pearson's ρ = -0.112, *P* =0.241 flight, ρ = -0.065, *P* =0.504 activity), and accordingly they were neither affected by wind nor whether the wolf was approached by one or two persons (since the tolerance distances were).

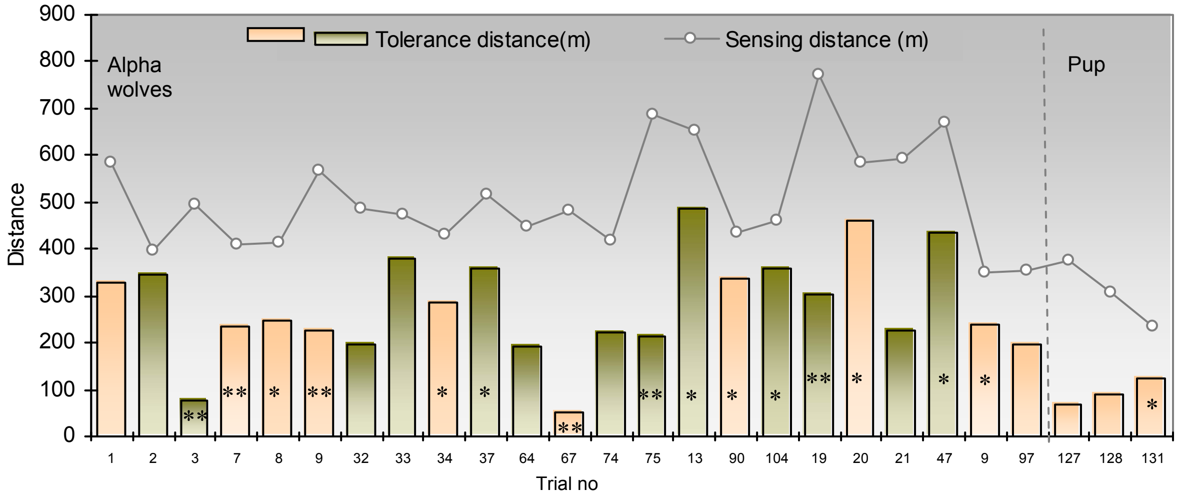


FIGURE 6. *Sensing- and tolerance distance of gray wolves approached by one (orange bar) or two (green bar) persons, south-central Scandinavia 2001-2002. The observations illustrated are only a sample (N = 26) of the 125 total trials. In the other trials, no separate sensing distance was registered. * and ** indicate trials in a tailwind and a headwind, respectively. If no *, there was no wind.*

a. A descriptive account of their behaviour

The wolves behaved in one of three ways when they were approached: **either** they ran straight away, **or** they ran away, but returned when the disturber left the area, **or** they moved in a half-circle around the disturber. No wolf ever moved towards and confronted the approaching person (Fig. 7a-g).

In 83% of the 125 trials, the wolves ran straight away. I have then considered trials where a wolf moved 90° from the disturber, but without getting closer, as a 'run straight away' behaviour. To be 'half-circling', at some point the wolf had to get closer, or maintain the original distance, to the person who approached it. Using these definitions, the wolves half-circled in 5% of the trials, but only the Våler male showed this behaviour. However, in some trials the pups showed a somewhat similar version. The pups did run away, but in doing so, they went around the disturber, thereby crossing the human track. No alpha wolf ever did that. In the remaining 11% of trials, a wolf first ran away, but then returned as soon as the disturber left the area. The pups, however, never returned.

The wolves showed the same flight patterns in trials where the disturber did not stop after fleeing the animal (N =11, three trials on each alpha wolf, and two on the pups).

The Rømskog female twice behaved in a way that does not fit into any of the three categories above. I will discuss her behaviour in detail later.

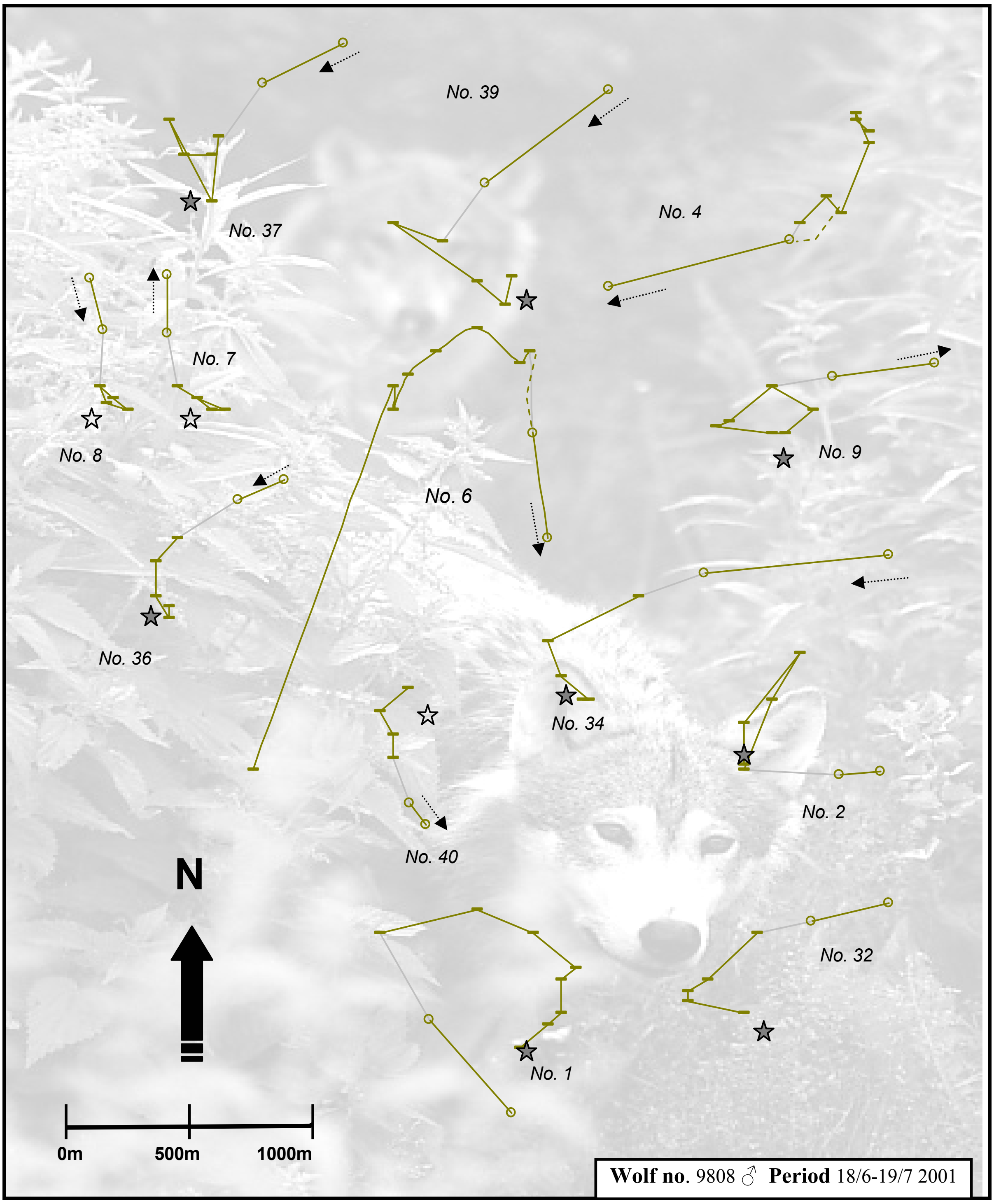


FIGURE 7a. *Movement of a gray wolf approached by a person, south-central Scandinavia 2001.* o *is start and stop of the person, horizontal bars* ▬ *are wolf positions while it moved away from its bed site (first bar after 2. circle). Not shown are 5 trials in which the wolf retreated < 200m. Note that the person did not proceed after the wolf moved, but withdrew in the same track as soon the wolf rested again (if not, the alternative route is indicated with* - - - - *). In trial no. 2, 7, 8, 9 and 37 the person withdrew immediately.*

······► *Direction of wind. If no arrow, there was no wind during the trial.*

★ *Location of pups, based on vocal signals.* ☆ *Pups in vicinity, location not known.*

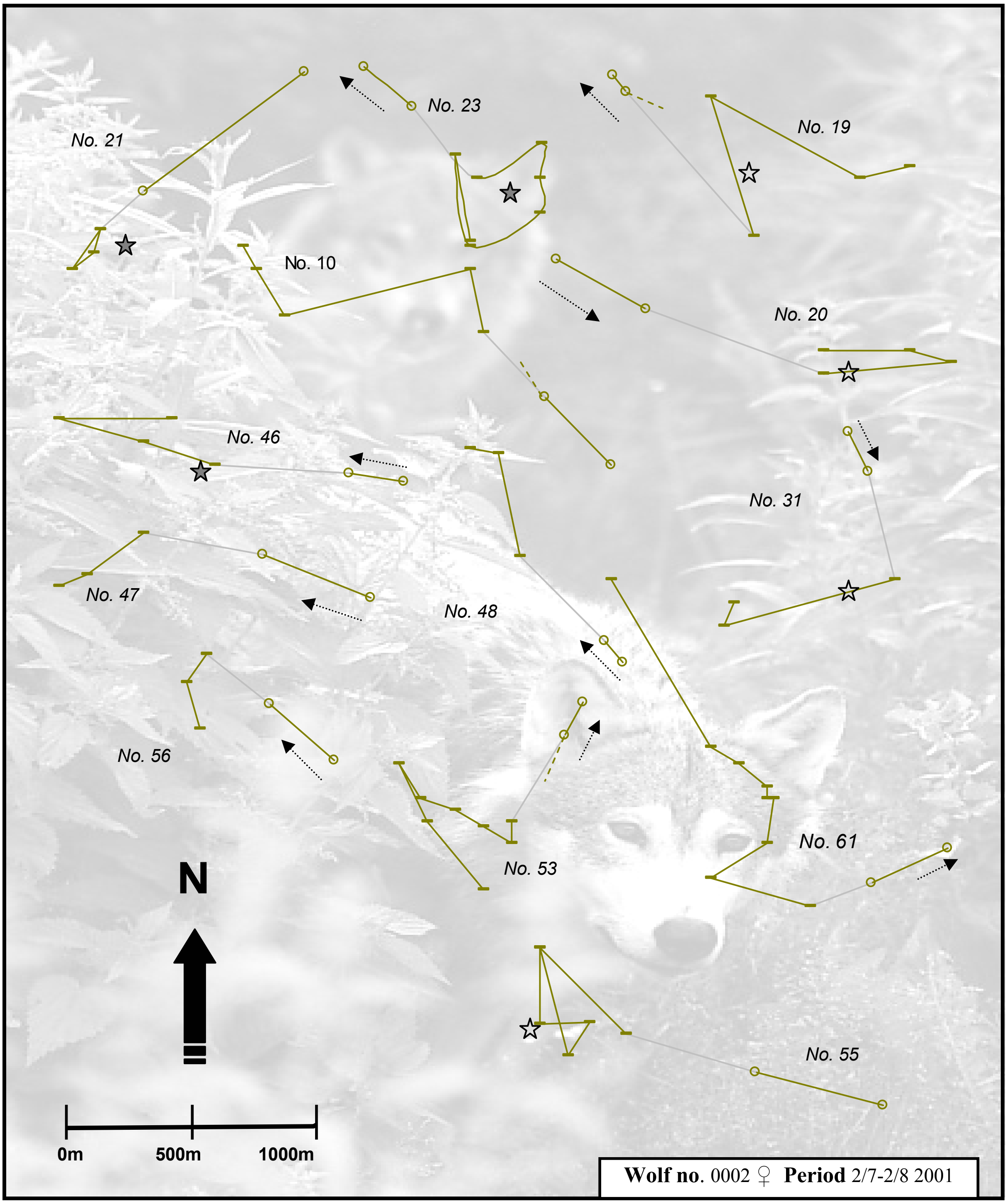


FIGURE 7b. *See text in Fig. 7a. Not shown are 2 trials in which the wolf retreated < 200m and 3 trials where triangulation was not sufficient to trace all movement of the wolf. In trial no. 19, 20, 21 and 23 the person withdrew immediately.*

⇢ *Direction of wind. If no arrow, there was no wind during the trial.*

★ *Location of pups, based on vocal signals.* ☆ *Pups in vicinity, location not known.*

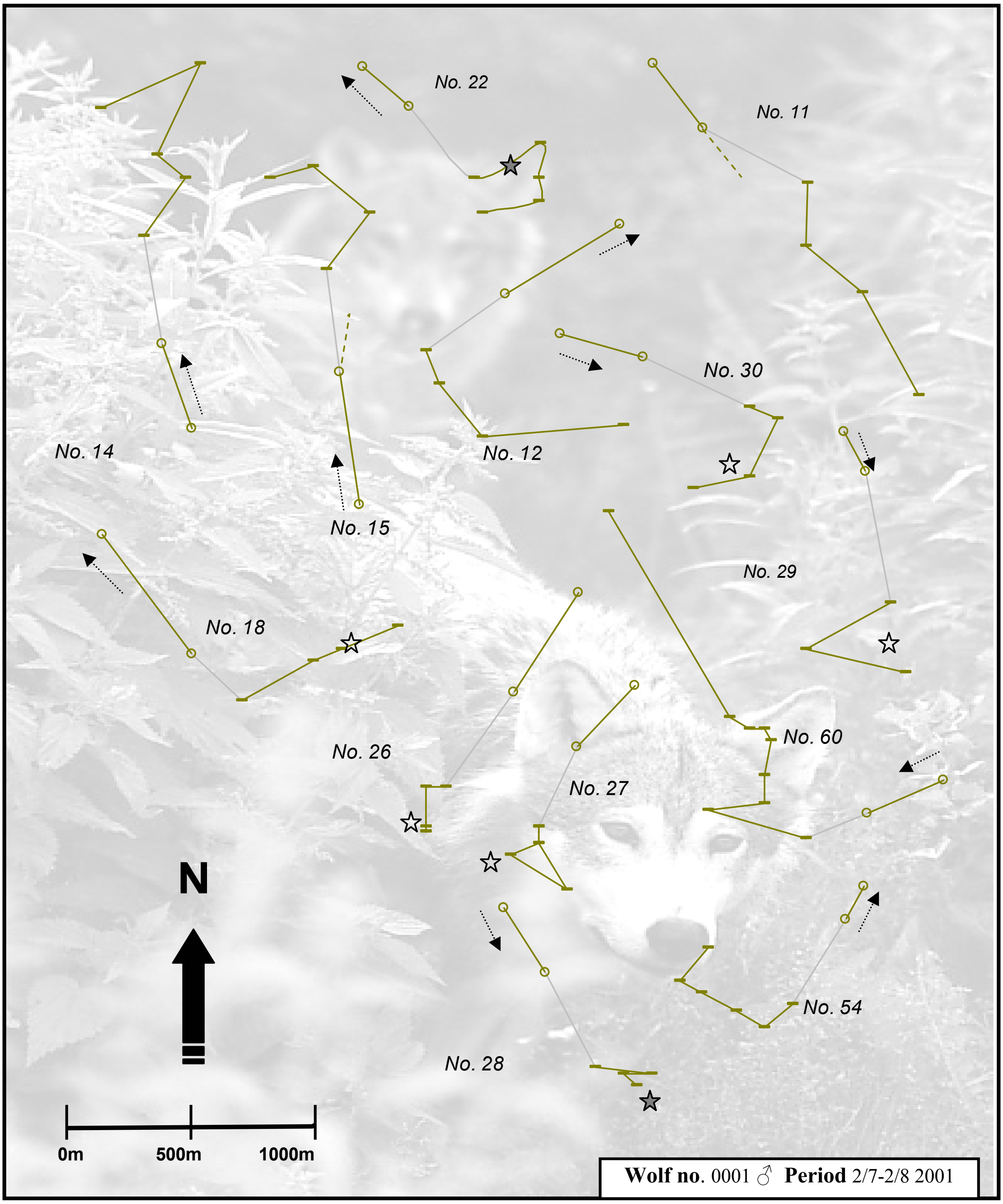


FIGURE 7c. *See text in Fig. 7a. Not shown are 2 trials in which the wolf retreated < 200m and 3 trials where triangulation was not sufficient to trace all movement of the wolf. In trial no. 18, 22, 26, 27 and 28 the person withdrew immediately.*

⇢ *Direction of wind. If no arrow, there was no wind during the trial.*

★ *Location of pups, based on vocal signals.* ☆ *Pups in vicinity, location not known.*

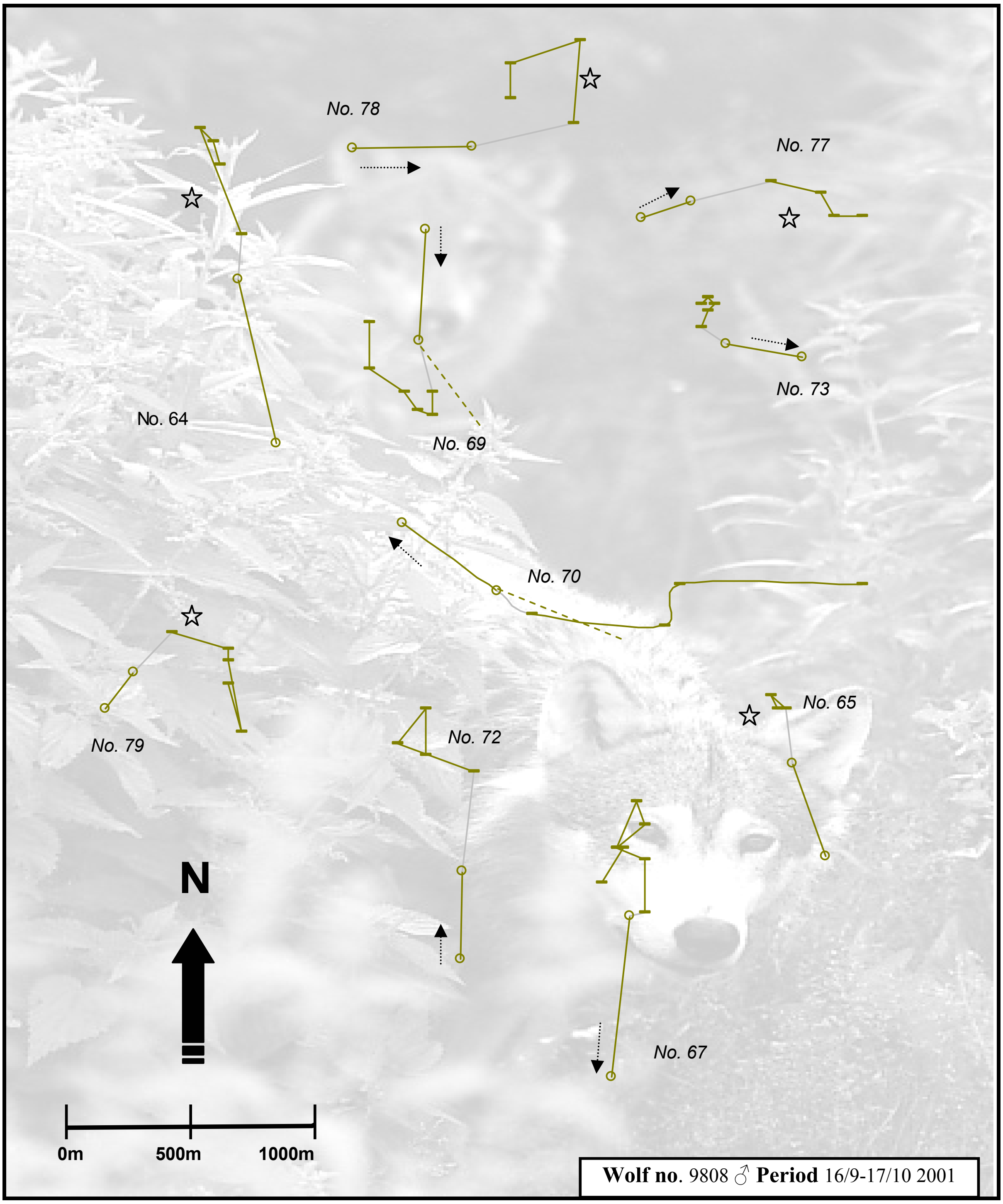


FIGURE 7d. *See text in Fig. 7a. Not shown are 5 trials in which the wolf retreated < 200m, and 3 trials where triangulation was not sufficient to trace all movement of the wolf.*

⇢ *Direction of wind. If no arrow, there was no wind during the trial.*

☆ *Pups in vicinity (based on scats and/or observation), but location not known.*

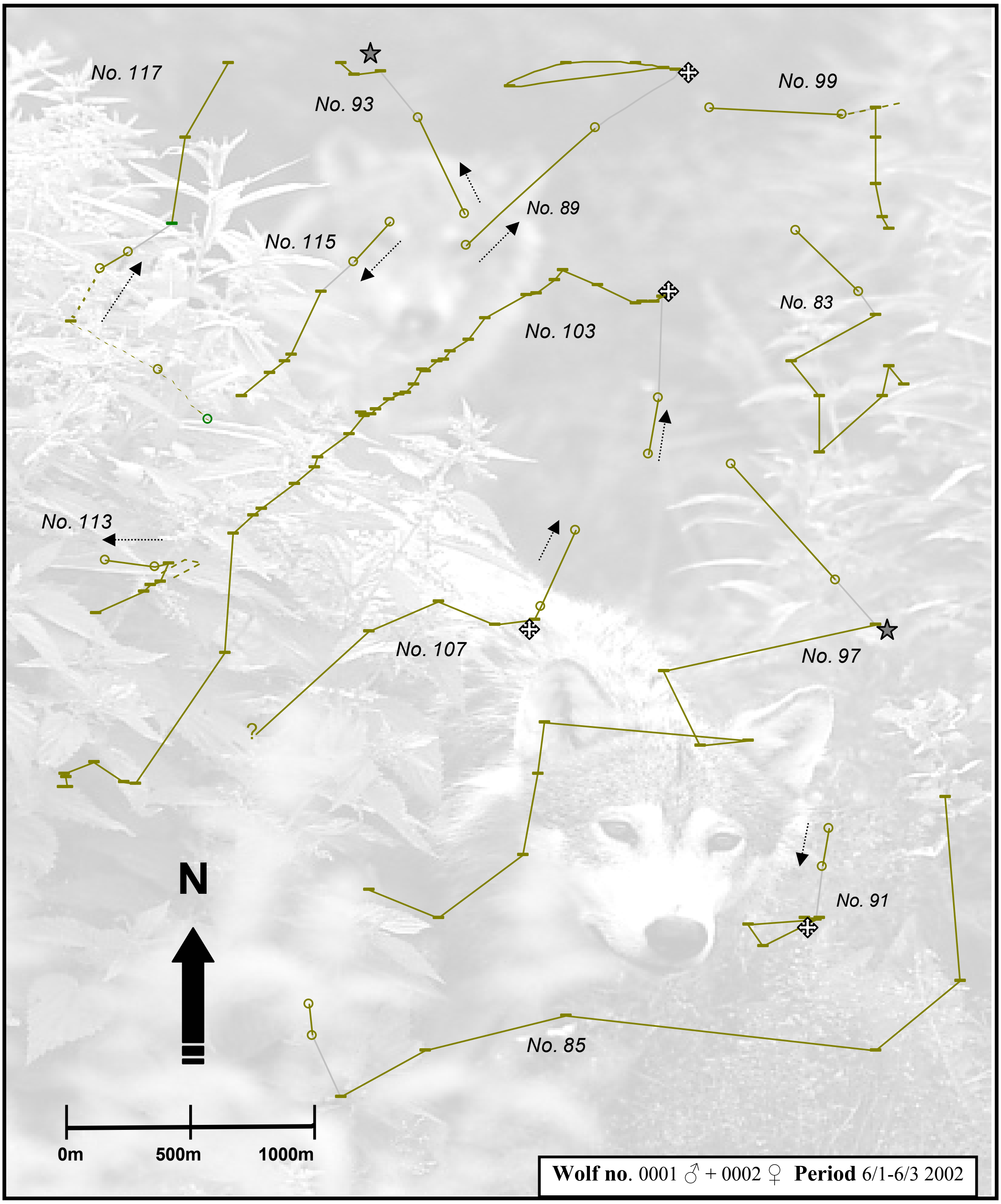


FIGURE 7e. *See text in Fig. 7a. Not shown are 2 trials in which the wolf retreated < 200m and 3 trials where triangulation was not sufficient to trace all movement of the wolf. In trial no. 89, 91, 103 and 107 the person withdrew immediately.*

⇢ *Direction of wind. If no arrow, there was no wind during the trial.*

★ *Location of pups, based on tracks in snow.* ✥ *Fresh kill (moose Alces alces 7/1-02).*

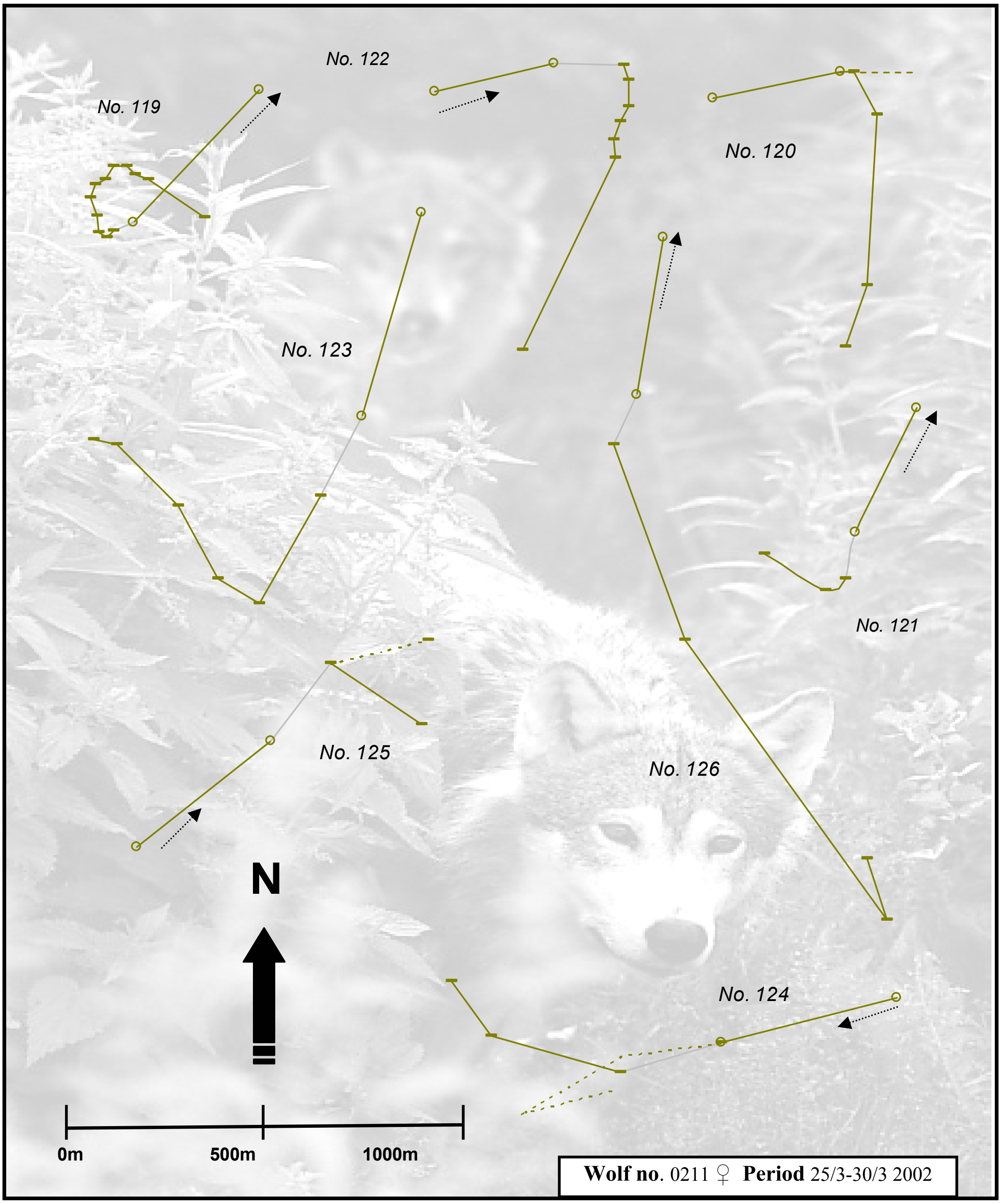
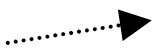


FIGURE 7f. *See text in Fig. 7a.*



Direction of wind. If no arrow, there was no wind during the trial.

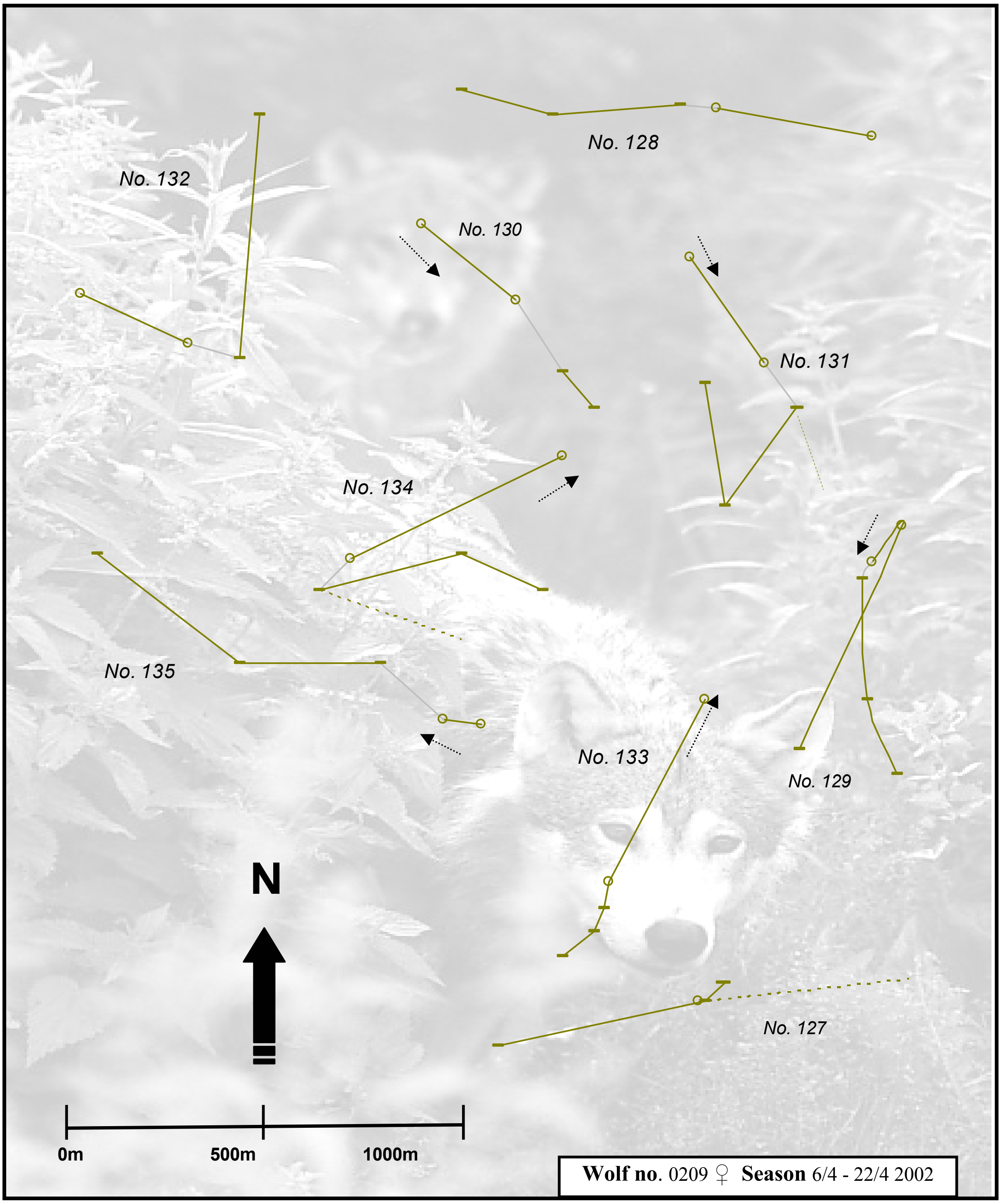


FIGURE 7g. *See text in Fig. 7a.*

Direction of wind. If no arrow, there was no wind during the trial.

b. Fleeing distance and time spent active.

Overall the alpha wolves both moved the same median distance (308 ± 114.5m Våler, and 337 ± 227.1 Rømskog) and spent the same time active (8 ± 2.5 min Våler, and 9 ± 4.0 min Rømskog) after being disturbed (N =92, Mann-Whitney *W* =4231, *P* =0.439 for flight, and *W* =4234, *P* =0.448 for activity), although it varied more for the Rømskog pair (Fig. 8).

However, they did not show the same change of behaviour between the two periods of different pup vulnerability: Their median fleeing distance did not differ in the two periods (N = 92, *W* = 901, *P* = 0.369), but **the range** of how far they moved in the second period, **tripled** for the Rømskog pair (from 0-1588m in first to 0-4900m in second), while it was **halved** (from 0-2071m in first to 127-1182m in second) for the Våler male. Also, the pair spent the same time active in both periods (8 ± 3.3 min in first vs. 10 ± 4.6 min in second) (N =57, *W* =873, *P* =0.174), while the Våler male spent a shorter time active in the second than in the first period (6 ± 1.7 min vs. 10 ± 3.2 min) (N =35, *W* =424, *P* =0.002).

When disturbed, the pups stayed active for a longer time than the alpha wolves (16 ± 2.6 min versus 8 ± 2.9 min for adult wolves, N =109, *W* =5032, *P* =0.058). They also had a tendency to move a longer distance (502 ± 72.3m versus 335 ± 170.8m for adult wolves). However, due to a high variance, this was not significant (*W* =5158, *P* =0.308). Both the fleeing distance and the time spent active varied more for the pups than for the adults (Levene's test *P* =0.378 flight, and *P* =0.926 activity, which means the variances were **not** equal, and more so for activity than for flight).

iii. What type of bed sites did the wolves use?

The wolves used a total of 202 bed sites in this study. For a closer examination of the bed sites' habitat characteristics, I selected 58 pairs of corresponding sites where a wolf had rested before (α-sites) and after (β-sites) being disturbed. I first use α-sites to test for differences between individuals, and between the two periods of different pup vulnerability. I then compared the β-sites to the α-sites to look for effects of disturbing the wolves. Note that an α-site are a wolf's original bed site, which it in contrast to β-sites, had chosen **unaffected** by any acute human disturbance.

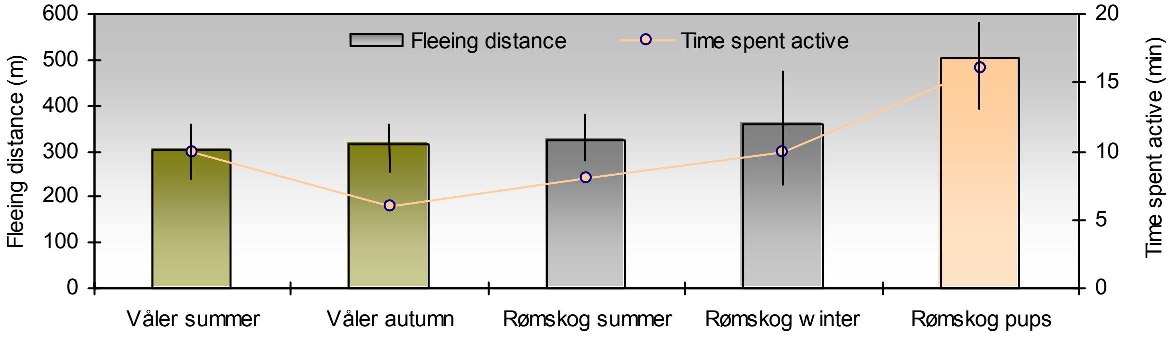


FIGURE 8. *Median ± SE fleeing distance and time spent active for gray wolves approached by humans, south-central Scandinavia 2001-2002. One alpha male was studied in Våler (N =35), one alpha pair (N =57) and two pups 10-11 months old in Rømskog (N =17).*

i. Bed sites used prior to being disturbed.

In six out of 58 α-sites, the wolves rested at a terrain level less than 70%, which means that in **nine out of ten** days they lay on or near the top of a hill. On the very top (i.e 100% level), the wolves rested on 65% of the days. On no occasion did the Våler male rest at a level below 75% (N =20), while the Rømskog pair only bedded below 50% when they had a fresh moose kill (three times out of 34, omitted as outliers in the analyses).

The field of vision from sites ranged from 22 to 875 m (median 180 m Våler, 293 m Rømskog), and was correlated with the terrain level (N =116, Pearson's ρ =0.374, *P* =0.000). **I therefore combined the two into one relative index** called "To detect":

To detect = terrain level*field of vision/
median of all α-sites within territory.

This made possible comparisons between the two territories, which originally are too different to be compared directly. Values of "To detect" >1 indicate relatively more overlooking sites, and values < 1 more secluded sites.

There was no difference in "To detect" between the alpha wolves (N =51, W =496, *P* =0.650), while the pups used sites with a lower value (N =58, W =1594, *P* =0.017) (Fig. 9). Neither was there any change in "To detect" for the alpha wolves between the two periods (N =51, W =841, *P* =0.253), though there was a tendency for them to use sites with a lower value in the second period (N =20, W =127, *P* =0.116 Våler, and N =31, W =359, *P* =0.067 Rømskog).

The vertical cover on sites ranged from none to full cover, while the canopy coverage ranged from none up to 80 % (median 20% in Rømskog, and 30% in Våler for both cover and canopy coverage). I also combined these two parameters into one relative index, and called it "To hide":

To hide = [cover+canopy] /
median all α-sites within territory.

Values of "To hide" >1 indicate relatively more, and values <1 less secluded sites.

For alpha wolves there was neither any change in "To hide" between periods (N =51, *W* =106, *P* =0.234), nor between individuals within one period (N =51, *W* =192, *P* =0.521 first, and *W* =119, *P* =0.819 second period). The pups bedded at more covered sites than the adults when both periods are taken together (N =58, *W* =287, *P* =0.029), but not significantly more covered than the alpha wolves bedded in the second period (N =27, *W* =121, *P* =0.106).

ii. Bed sites used after being disturbed.

After being disturbed, all alpha wolves chose a more secluded bed site than the original one (Fig. 9). The pups, however, showed no significant changes neither concerning "To detect" (N =14, paired Sign *P* =0.227) nor "To hide" (N =14, paired *t* = -1.50, *P* =0.092). Though, there was a tendency for them to settle again on more covered sites. Fig. 10, next page shows the 'typical' bed sites used by alphas before and after a trial.

The preference for a more secluded site was stronger for the Rømskog pair than for the Våler male. After being disturbed, the pair chose less overlooking sites in both periods (N =62, paired Wilcoxon Sign Rank *W* =396, *P* =0.002) and settled on more covered sites (N =62, *W* =351, *P* =0.005). The Våler wolf, however, behaved more like the Rømskog pups. After being disturbed, it only showed a significant preference for more "To hide" in summer (N =22, paired Sign *P* =0.021) and less "To detect" in the second period (N =18, W =42, *P* =0.012). (Table 7, Appendix B shows values and test results for the original habitat parameters, not only the combined indices).

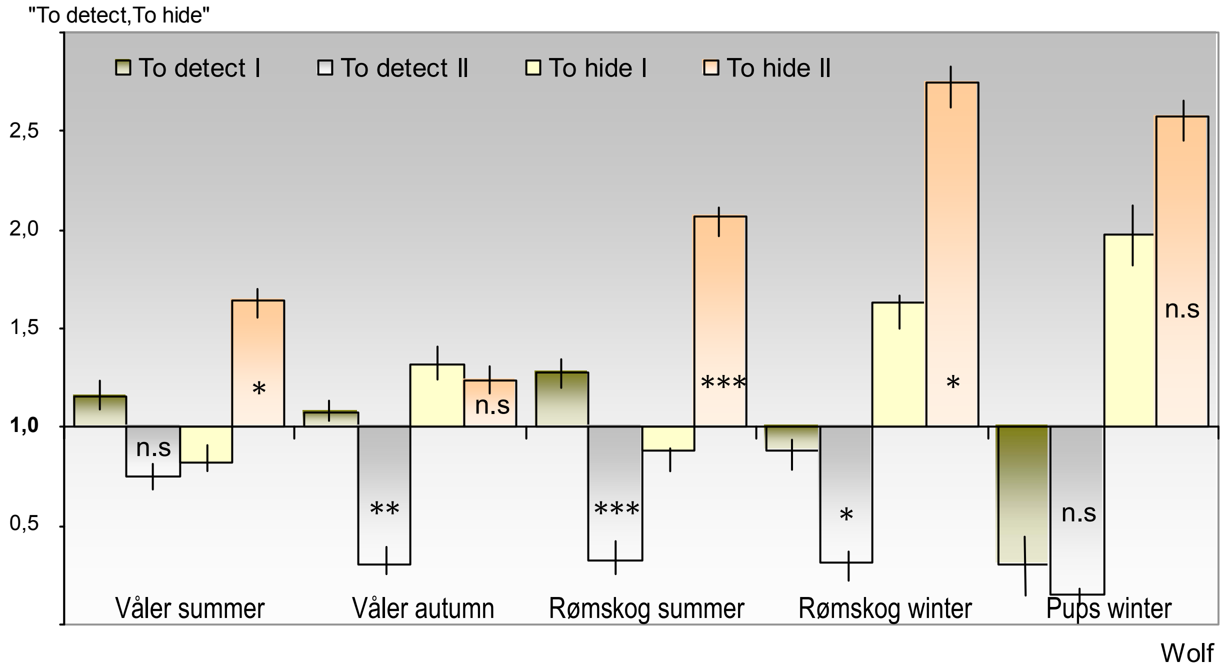


FIGURE 9. *Bed sites for gray wolves, before (I) and after (II) they were disturbed by a person, south-central Scandinavia 2001-2002."To detect" is a combined index of terrain level (0-100%) and field of vision (m). "To hide" is a combined index of horizontal cover and canopy coverage (both 0-100%). One alpha male was studied in Våler (N=20), one alpha pair (N=31) and two 10-11 months old pups in Rømskog (N=7). Sites were triangulated with an error ≤ 20 m.*

a)

View

Blånende åser

Nærbilde

Åpen furukolle i sol

b)

View

Overflate granbestand
10-20 år

Nærbilde

Tettsjikta gran m gras

FIGURE 10. *A typical bed site for gray wolves a) before and b) after being disturbed by a person in a study of the wolves' tolerance to humans, south-central Scandinavia 2001-2002.*

IV. DISCUSSION

a. No need to fear wolves in the Scandinavian forests?

To tell the end of the story first; Little Red Riding Hood was not eaten by the Wolf in my study. Instead we spent 756 hours < 1 km from wolves, and an additional 452 hours at unknown distances inside the wolf territories, without experiencing any aggressive behaviour from the 18-22 wolves present there.

That is not to say that wild wolves in Scandinavia will not attack a human. However, it indicates that presently the chances are diminishingly small. Actually, according to my data, the chance for a hiker to be confronted by a wolf in Scandinavia, is **nil** ($N = 125$, $Z = 22.99$, $P = 0.000$). The wolf knows about a hiker long before the hiker can detect the wolf, and the animal runs off without being seen. To get wolves at a close range, I believe one has to sit still or put an effort into it by sneaking up on them.

The person monitoring the wolf during a trial **was** sitting still, and on several occasions the wolf did approach this person after leaving its bed. Not only is a person sitting still harder to detect than one walking through the forest, but also the wolf may not be as alert when it is moving as when it is resting. Still, the wolf always sensed also this person before exposing itself, and immediately broke off the trail. However, from anecdotal observations we know that a wolf can come up close before it realizes the presence of a human (e.g. 5m, the Våler male in a strong and rainy headwind, pers. obs.).

A summary of human encounters with another potentially dangerous northern carnivore, the brown bear *Ursus arctos,* revealed three situations in which it is more likely that the animal might defend itself: when it is wounded, when it has cubs, or when it has a carcass (Swenson *et al.* 1999). We approached wolves in all these situations: at rendezvous sites, on fresh kills and we even disturbed a crippled wolf (the Rømskog male had only three legs functioning, pers. obs). Although none of the wolves ever confronted the disturber, the Rømskog female twice showed a behaviour with elements of defence:

The first time we approached her on the pack's earliest rendezvous site (8th of July), **she** approached **us** from a distance of about 650 m, but turned back as the disturber started to walk towards her (trial no. 19, Fig. 7b). On the next day, in the exact same setting (trial no. 23), she followed the disturber back for a short distance after first running off in the opposite direction. The other five times we approached her at a rendezvous site, she ran straight away. Clark (1971) and Mech (2000) both found that pup protection was initiated by the breeding female. The Rømskog male was present during these trials, but did not move. For the pack-living wolf, a division-of-labour is expected, although the specific duties for each pack member vary (Mech 1999).

Others have reported that wolves at the den try to fend off human intruders by barking (see e.g. Murie 1944, Scott *et al.* 1985, Peterson 1995), and in Canada and Alaska several biologists have experienced defensive wolves when intruding on their den (for a review see McNay 2002). Although we did not approach the wolves at their den, we did approach them as early as 18th of June, when the pups were still within 500m from the original den. Whether the pups lie inside the actual den or they are outside on an early rendezvous site, I believe makes no difference to the parent wolves. Either they will defend them or not. The alpha wolves in my study chose the last alternative.

When approached with pups nearby, the parent wolves ran away at a distance of hundreds of metres (mean 290m Våler, 393m Rømskog), and they ran off too far to eventually protect their pups (mean 357m Våler, 464m Rømskog). Would they have **come back** if we had proceeded all the way towards their pups? Certainly they always returned as soon as the disturber started to move back (Fig. 7a-c). On some days the wolves rested not right by their pups (based on pup vocalizations), but 200-500m away. When we then approached them, they actually ran **to** their pups, which indicates that the decision to **leave** the pups when approached in their vicinity is not a distraction strategy to confuse the intruder. It rather seems as they abandoned their pups for the safety of themselves. If so, they most likely would not return to protect the pups even if we had proceeded all the way.

The behaviour of the Rømskog female suggests there is a chance to encounter defensive wolves also in Scandinavia *if* intruding on their den. Though, the chance of accidentally intrude on a wolf den must be considered very small. At the population level, a sample size of three alpha wolves is too small, so more parent wolves should be studied before a final conclusion is drawn on the issue.

b. When and with which of its senses does a wolf detect dangers?

The wolves' mean tolerance distance (TD) in trials with no wind, normal ground conditions and only one person disturbing might be considered as their 'basic' TD =198m. Though, it will vary periodically due to intrinsic factors. In comparison, TDs for the Scandinavian lynx *Lynx lynx* have averaged 50m (Sunde *et al*. 1998), and for the Swedish roe deer *Capreolus capreolus* 240m (Cederlund & Näslund 1979). External factors like wind, topography etc. will cause deviations from the wolves' basic TD. For example were the three shortest TDs in my study (trial no. 108, 114 and 119) all in headwind trials on soft snow with the wolves 'hidden' behind a small hill-top.

In one quarter of the trials I recorded a sensing distance (SD). The corresponding waiting distance could indicate that the animal awaited the situation having full control, but considered it yet not critical. However, it is more likely that it reflects the time a wolf needed to determine it was approached by a person. For the first alternative, my data indicate that the wolf did not stand motionless 'considering' the situation. Rather it got restless, and the activity change in its radio-signals was not brief like those I categorized as a SD, but lasted until the wolf eventually ran away. I observed this last type of behaviour in 28 trials: the wolf only moved within 25m of its bed until the disturber drew closer, whereby the animal finally ran away. The lapse of time from sensing to fleeing in these trials, is of course also a waiting distance. Though, I did not include them as such, so that I could distinguish them from the SD waiting distance.

It can be argued that the SDs were only random movements. However, wolves can lie motionless for hours when resting during the day (see e.g. Murie 1944). In the initial phase of each of 119 trials, I monitored the wolves for an average of 34 continuous minutes without any sign of activity. In the remaining 6 of the 125 trials, the radio-signal indicated a brief activity at such a long distance (847 - 1311m) that I discarded them as random movements. Since I also found significant patterns in the SDs (effects of wind and noise), I do not believe they were just random movements.

Why was a SD not registered in all trials? One explanation might be that the movement a wolf makes to stand or sit up from lying down, creates only a slight and very brief change in the radio-signals. I might have missed some SDs that were faint enough to pass between two pulses of a signal. However, another explanation may be that the wolves' reaction varied depending on whether it detected the person with its smell, or its hearing. Therefore, the lapse of time that passed until the wolf ran off varied, assuming that the wolves were familiar enough with the human scent to immediately recognize it, but from hearing a person they could not straightaway determine it.

Certainly the wolves did not **only** use their hearing **or** their smell to detect people: First, a wolf cannot possibly tell from foot steps alone 479m away (the longest TD when approached by one person), that this is a human. Secondly, if the wolves used only their smell, their TDs should not be influenced by sound, which they were in my study (Table 6 and Fig. 5). Hence, my data falsifies both alternatives. The wolves sometimes detected the person with their smell, and sometimes with their hearing. Can my data tell **when** the wolves used which sense? Although my study was not specifically designed to test the wolves' senses, some observations are of interest:

The SDs were registered 13 times when the disturber was one person vs. 14 times when two persons, which suggests that it was not the human voice that alarmed the wolves in trials where they not immediately fled. Then either it was some other noise, e.g. the breaking of dried wood on the forest floor, or it was a human scent too transient to be determined.

Wolves hear sounds up to 80 kHz (Asa & Mech 1995), and can apparently hear the howls of other wolves at 6.4 - 9.6 km away (Harrington & Mech 1979). Ultrasound (sound above 20 kHz, not detectable for humans) is easily absorbed (Lawrence and Simmons 1982), while infrasound (sound below 20 kHz) is carried over long distances (Reimers 2001). Naturally, we do not know the specific action of all sounds through different terrains. However, I assume that the noise from breaking dry wood has a lower frequency than the human voice, which may explain the only small effect of two persons on the TDs, but the many trials marked for a noisy ground coinciding with a SD registered.

Dogs smell 100 - 10 000 times better than humans (Moulton *et al.* 1960, Moulton & Marshall 1976), and it is generally assumed that the olfaction of the wolf certainly is no less than the dog (Asa & Mech 1995). Physically it is possible that wolves can pick up the human scent at ½ - 1 km even in a rugged terrain, and if so the SDs in a tailwind were due to the wolf having sensed something, but then receiving too few molecules to ascertain the scent was human. Although we lack the knowledge to say how likely it is, it seems reasonable that there is a threshold of molecules needed for the wolf to determine the origin of a scent.

The wolves had **longer** waiting distances in a headwind than in a tailwind (Fig. 6). A plausible explanation is that they then did not receive the scent molecules necessary to detect the disturber by smell, but instead were alerted by a sharp noise as the person walked through the forest. The other alternative; that the wolves did smell the disturber, but the scent was too transient to determine, is not very likely in a headwind.

To sum it up; the most important environmental factor influencing the wolves' TDs was the wind. In a strong tailwind, they may have picked up the human scent from at least 600m (the longest SD in this study), but not sufficiently to determine it came from a person. In a strong headwind, however, I believe a sudden noise of low frequency alarmed the wolves before they smelt the person. They therefore showed a relatively longer waiting distance, if this is considered to be the lapse of time until the confirming scent also reached them. There were, however, few SDs registered, and they should be interpreted cautiously.

c. How have the wolves adapted to living in a human environment?

i. Their behaviour

The alpha wolves’ fleeing strategy when approached suggests they did not move around more than necessary to avoid the disturber (they stayed active for about eight minutes and fled a mean distance of 325m). I consider this to be a product of both evolution and individual learning capacity, with the latter being the more important:

Instinctively a wolf in Scandinavia today knows it should avoid an approaching person, as the wolves surviving the last century must have been the shyest animals. However, a wolf also knows from experience that it can accidentally encounter other humans when it runs off, particularly during day-light. Depending on the human activity within its territory, a wolf has a varying incitement to channel its activity to the night and avoid movement during daytime (see e.g. Vilà et al. 1995, Ciucci et al. 1997, and for the Våler male see Gustavsen 2002).

Through experience a wolf learns to optimize its behaviour. Lack of experience therefore may explain why the pups behaved less determined than the adult wolves: they stayed active for twice as long, they moved a longer distance, and there was a greater variation both in their fleeing distance and their flight route (Fig. 7, 8).

An unequal incitement to avoid daily activity likely led to the two differences between the Våler male and the Rømskog pair in their periodical change of behaviour: **First,** in the wolves’ TDs there was a downward trend between periods for the Rømskog pair, while there was no such trend for the Våler male (Fig. 11).

Since wolves in Våler are frequently exposed to people, it becomes important for them not to overreact, more than for wolves in Rømskog. Hence, the Våler male‘s TDs were **even**, while the TDs of the Rømskog pair more reflected their different vulnerability, i.e. they were more on guard or less tolerant with site-depentdant pups than without. This could be due solely to the presence of pups, or the pups in combination with a higher human activity in summer.

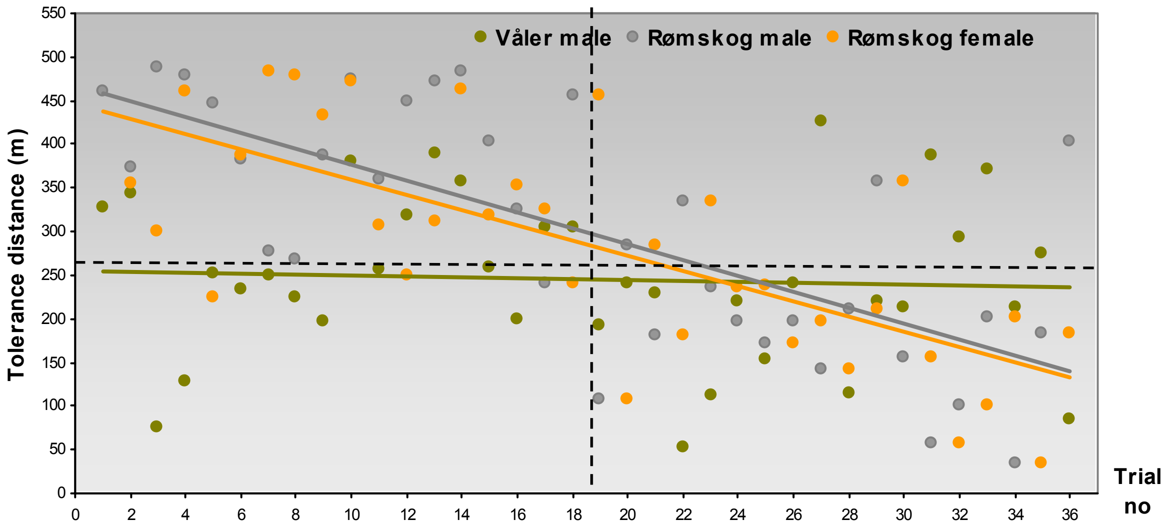


FIGURE 11. *Trends in gray wolves’ tolerance distance to approaching persons, south-central Scandinavia 2001-2002. Two territories with a different level of human impact; Våler with a stronger impact relative to Rømskog. All wolves were alpha animals. The dotted vertical line indicates two separate periods in wolf life; with and without mobile pups. The dotted horizontal line is the mean tolerance distance.*

Though, ten percent of the TD reduction for the Rømskog pair is due to four trials on a very soft ground in the second period, which lowered the average TD for headwind (see chapter IV a. ii). Still, there is a 50% reduction that most likely is due to the Rømskog pair being less on guard when their pups could easily escape together with the pack. I see no other reasonable explanation. If e.g. the temperature had influenced the smell of the disturber, the wolves' TDs should have been shorter in summer when there are higher levels of human scent (all scents) in the terrain.

Within one period there was no trend for any wolf in their TDs. Hence, they did not show any short-term habituations to being disturbed.

Secondly, the Våler male who inhabited the territory with a higher human activity, settled quicker when disturbed in the period when his pups were able to follow. The Rømskog pair actually was active for longer when disturbed in the second period, and the range of their fleeing distances tripled (Fig. 8). The general day activity of the Rømskog wolves also increased in the period (Skandulv, unpubl. data), which explains their higher activity also when disturbed. The wolves were about to go hunting, and restless.

Irrespectively of the differences between the wolves, their fleeing distances and the time spent active were of low levels. This is likely an influence of evolution. When disturbed, all animals use energy that makes up an additional cost in their original activity budget (Reimers 1980, Fancy 1983, Murphy & Curatolo 1987, Andersen *et. al* 1996). This holds also for the gray wolf, although not crucial since it can be considered the archetypical endurance athlete (Constable *et al*. 1998).

One part of the alpha wolves' behaviour did not differ: their fleeing strategy clearly depended on whether they had something to lose by running away. When their pups were site-dependant, the alpha wolves were reluctant to leave the site, and returned almost on the exact same second as the disturber started to move back. As the pups got old enough to follow, the alpha wolves no longer returned (Fig. 12).

A litter of pups represents one year's reproductive investment, and the wolf has to choose whose safety it should value the most; its own or its pup's. As the wolf is a repetitive breeder, the former is expected. Also, the history of being persecuted by guns has likely favoured the animal that does not stay to protect its pups, and so the strategy 'not to stay' is an evolutionary adaptation. The Rømskog pair also returned when they had a fresh moose kill, but no longer as the kill got pre-emptively consumed. (The few returns seen for period II in Fig. 12, are all moose-kill trials). The two pups never returned.

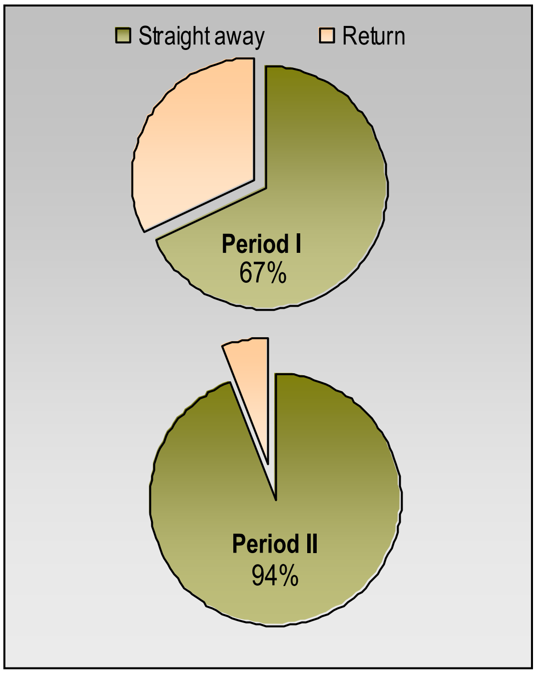


FIGURE 12. *Proportion of trials in which alpha wolves returned to their bed site after being disturbed by humans, Scandinavia, 2001-2002. N =72. In period I, the wolves had pups too young to follow the pack as opposed to in period II.*

ii. Their bed sites

The wolves showed one more interesting adaptation: their choice of bed sites clearly indicates a strategy to detect potential dangers before being surprised by them. The habit of lying on a hill-top was so consistent for the alpha wolves one can suspect it to be instinctive knowledge. Though, since the pups rested more randomly, I believe it is knowledge achieved at least partly through experience. Most hikers in the forest namely follow paths and truck-roads, which normally are laid along valley bottoms. To stay at a hill-top then, does not only increase a wolf's chance of detecting people, it also lowers its chance of being disturbed by them in the first place. There might of course be additional reasons why wolves rest at hill-tops, e.g. to get the physical space to socialize.

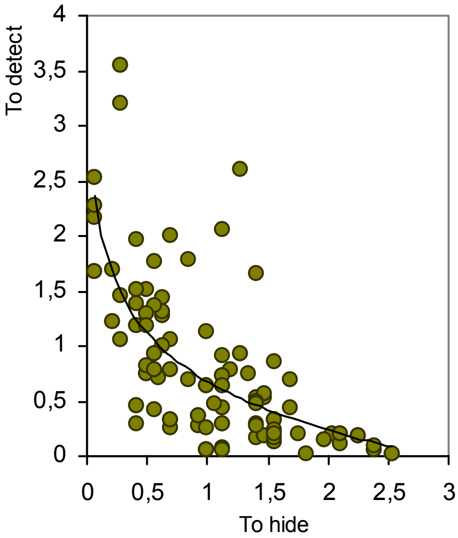


FIGURE 13. *Gray wolves must choose between how overlooking ('To detect') and how covered ('To hide') their bed sites are, as the two parameters are negatively correlated. 'To detect' is a combined index of terrain level(0-100%) and field of vision (m). 'To hide' is a combined index of canopy coverage and horizontal cover (both 0-100%). The indexes were made relative so that 1 is the average value for all registered wolf bed sites within a territory. Data were gathered during a behavioural study testing the wolves' tolerance to humans, south-central Scandinavia 2001-2002.*

Though, for a wolf there is a trade-off between detecting the dangers, and hiding from them (Fig. 13). The hill-top is not the appropriate place to stay when a person does not follow the paths and valleys. The way the wolves sought hided bed sites after being disturbed, was just as consistent as their initial choice to rest at the hill-top. Though, the habit of seeking cover was stronger for the Rømskog pair than for the Våler male (Fig. 10). This could be due to differences in the terrain, e.g. that the distance from a hill-top to cover is longer in Våler than in Rømskog. However, the Våler habitat is rugged on a finer scale than Rømskog. Instead it may have been yet another result of the Våler wolf being more familiar with people. It felt more in control of the situation than the wolves in Rømskog did.

d. The wolf's potential to habituate to people.

The wolves in this study obviously perceived man as danger. However, we know from other areas that the human fear in wolves can gradually be lost; they become **habituated** to people. The most recent examples come from American national parks, where wolves around camp-sites have habituated to people after being fed by them (McNay 2002).

How quickly do wolves habituate? Is it necessary to hunt wolves to keep their human fear? The picture is ambiguous. It took e.g. L. David Mech one intensive summer to habituate an arctic pack enough to tolerate his presence (Mech 1988), while the wolves on Isle Royale have not habituated at all: among the total 15 000 visitors on the island, sightings of wolves were fewer than a dozen after three decades of not being hunted (Peterson 1979). After five decades, and no hunting, the wolves on Isle Royale remain fearful of man (Peterson & Vucetich 2002). Presently, it seems as human habituation in wolves occurs mainly when people actively seek to tame the animals.

A Russian study once found that although wolves initially avoided unfamiliar objects placed by the scientists near houses and farmyards, they no longer feared the objects after 10-15 days (Bologov, unpubl. data). My study also shows there is a marked difference between situations where wolves feel in control, and not. Two specific examples to illustrate the general: **I**. On the day of trial no. 55, the Rømskog female lay 80m from a dust-road without bothering about neither cars, bikers nor me walking along the road. However, as I stepped a few paces off the road and in her direction, the radio-signal indicated she got up immediately. I retreated back to the road, and she settled again after half a minute. I then repeated the procedure three more times and got the exact same reaction! **II**. Pup 0209 once sat apparently watching us standing beside the car from 350m across an old clear-cut. We were talking and triangulating. After 40 minutes we walked off the road and towards the wolf, whereby it immediately fled.

Accordingly, wolves that enter farmyards and go close to buildings in the absence of people (as e.g. the Våler male frequently did, Vold 2001), have not necessarily lost their fear of man *per se*. I believe this particular ability to judge a situation, and less respond to it by instincts, means the species is so mentally complex there is no fixed answer to how much aversive treatment is needed to keep the human fear in a wolf population.

CONCLUSIONS

The potential danger of the gray wolf to humans, can **never** be confirmed or condemned as either or. The species is simply too adaptive. However, by studying its members, we can picture the relative danger of a present population.

The wolves in this study not only showed several strategies to avoid human encounters, their individual differences also indicate a very high learning capacity. From their behaviour I conclude that my study wolves were shy animals that actively sought to avoid human contact. To what extent my conclusion also holds for the population as a whole, depends on whether one considers my sample as enough individuals to represent it. In the 125 trials in this study one fifth of all the wolves in Scandinavia were present, but in a population there can always be individuals behaving abnormal.

However, if my study animals behaved abnormal, they all did it, as their shy behaviour was very consistent throughout the study. Certainly, studies of more individuals will make the conclusion more robust, but for now, I conclude that overall the Scandinavian wolf population **is** shy. Unfortunately, there are presently no comparative studies from other populations. Therefore I cannot tell **how** shy the Scandinavian wolves are. Just for the curiosity, though; the non-hunted wolves of the pristine Mt McKinley, fled at 400m when legendary Adolph Murie first approached them (Murie 1944).

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